A revision of *Rutilaria* Greville (Bacillariophyta)

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CONTENTS

SYNOPSIS. Detailed descriptions of *Rutilaria* Greville and its species and subspecies are given, based on light microscopy and, for most taxa, on scanning electron microscopy. *Rutilaria* is characterized by the presence of a periplekton in the centre of each valve; this is a rimoportula with an external part consisting of a tubular stem from

the top of which two arms arise and encircle the stem of the periplekton of the sibling valve. *Syndetocystis* Greville and *Syndetoneis* Grunow are shown to be synonyms of *Rutilaria*. There are 28 species, five of which are divided into two subspecies. Thirteen new species and all five non-type subspecies are described as new, and two new combinations are published for the species hitherto placed in *Syndetocystis* and *Syndetoneis*. Only two species are found living, and both of these have fossil records. Six others are recorded with certainty from the Neogene, and the one sample in which another is found may be Neogene or Paleogene. Only one of the species with a certain Neogene record is not also known from the Paleogene. The living species are members of the neritic plankton and this is the probable habitat of most, perhaps all, of the fossil ones. The Rutilariaceae are a monotypic family, probably derived from the Hemiaulaceae and probably ancestral to the Cymatosiraceae.

INTRODUCTION

Diatoms of many genera, both recent and fossil, have their frustules united in inseparable chains. In almost all cases the structures that hold pairs of sibling valves together are spines modified to a greater or lesser extent, i.e. they are structures projecting from the frustule that are solid or, if hollow, closed. In *Rutilaria* Greville, however, there is in the centre of each valve a modified rimoportula that interlocks with that of the sibling valve. This is called the periplekton, a term proposed by Jurilj (1965), whose description of the structure was, however, very inaccurate. Externally the periplekton consists of a vertical hollow tube from the top of which two arms arise that encircle the vertical tube of the periplekton of the sibling valve. This can be seen by careful observation with the light microscope. Nevertheless, the first accurate description of the periplekton was that of Ross & Sims (1972), which was based on scanning electron microscopy. That the periplekton is a rimoportula with its internal opening a straight slit across a slightly raised papilla can only be seen by scanning electron microscopy. One can see with the light microscope that the monotypic genera *Syndetocystis* Ralfs ex Greville and *Syndetoneis* Grunow also have a periplekton with the same structure externally as that of *Rutilaria*, and this has been confirmed by scanning electron microscopy (see Plate I (b), (c), (e), (f) and Plate III (c) and (d)). This is by no means obvious from the published accounts and illustrations, which are either too inaccurate or too incomplete.

All species of *Rutilaria, Syndetocystis* and *Syndetoneis* are bipolar and bear at each pole an ocellus (see, e.g., Plate I (b), (f), Plate V (d), Plate VI (c), Plate XIX (d)). Although these are readily visible with the light microscope, the first mention of them was by Simonsen (1972), who reported their presence on the basis of information that I had given him. It was, of course, not until it became possible to examine diatoms with the scanning electron microscope that it could be seen that the structure at the poles of these genera is a plate penetrated by porelli and thus similar to those of such genera as *Auliscus* Ehrenb. and *Eupodiscus* J.W.Bailey, although without the thickened surrounding ring present in them.

It was rather more than forty years ago that these facts came to my notice. Amongst specimens from the upper Eocene deposit at Oamaru, New Zealand, that I was identifying was one of *Syndetocystis grevilleanus* Walker & Chase, the earliest name for the type species of *Syndetocystis*. When I realized that this specimen might belong to that species, I examined both the original material and the published descriptions and figures. This showed that the only accurate and comprehensive description that had been published by then was that in the protologue of the generic name (Greville,

1866), which did not include an illustration. All the subsequent descriptions and figures under various specific names were either inaccurate or incomplete. Examination at the same time of specimens of *Syndetoneis amplectans* (Grove & Sturt) Grunow and *Rutilaria radiata* Grove & Sturt, both present in the same fossil material, showed that none of the characters that distinguished these two species from one another and from *Syndetocystis* were a sufficient basis for generic separation. They differed only in: height of the vertical tube of the periplekton and the shape of its arms; height of the elevations at the poles; arrangement and size of the areolae; situation of spines.

Examination of other species of *Rutilaria* showed that all of them had an ocellus at each pole and a periplekton of similar structure. The two arms of the periplekton are equal in *Syndetocystis grevilleanus, Syndetoneis amplectans* and *Rutilaria radiata*, but in many of the other species of *Rutilaria* the two arms are dissimilar, one being longer than the other and differently shaped (cf. Plate III (d), Plate XII (b), Plate XIX (b), Plate XX (d)). This difference, like those listed above, is an insufficient basis for separation at generic level, and it is clear that all the species with a periplekton belong to a single genus. No detailed accurate description of this genus has been published, the nearest approach to this being the account of *Rutilaria* provided by Round, Crawford & Mann (1990), who also give a description of *Syndetoneis amplectans* under the name *Syndetocystis*.

In some species of *Rutilaria* the diminution in size of the valve with successive vegetative divisions is accompanied by very considerable changes in outline, greater than those in any other genus. The largest valves have an elliptical or sub-hexagonal central portion and capitate or subcapitate projections each twice as long as the central portion or even longer; the smallest valves are without projections and are similar in shape to the central portion of the larger ones (see Figs 19, 76). Whilst there is thus great difference in length between the largest and the smallest valves, the difference in width is small. As a consequence of this wide range in the outline of the valves, more than one name has been and is still applied to these species. This, and the existence of a number of undescribed species, made the need for a taxonomic revision obvious. It was also a necessary preliminary to establishing which, if any, of the species might be useful in stratigraphy.

The great increase in our knowledge of the morphology of diatoms resulting from the use of the electron microscope has shown the inadequacy of the system of classification previously accepted for them. A number of suggested revisions have been put forward (Simonsen, 1979; Glezer et al., 1988; Round, Crawford & Mann, 1990), but they differ very considerably and no consensus has yet emerged.

The relationships of *Rutilaria* are far from obvious and need to be examined in the light of a detailed and accurate account of its morphology. There are thus many reasons why a monograph of the genus is required, and it is hoped that this account, started long ago and now completed after many interruptions, will go some way to meeting those needs. It is, however, to some extent at least, an interim account rather than a final one.

There are illustrations in the literature of specimens that appear to belong to three different species of which I have not myself seen specimens (see pp. 63–64). This is, however, not the main reason for considering this as an interim account. *Rutilaria* is primarily a fossil genus; only two of its twenty-eight species are known living and both of these have fossil records. In all the fossil deposits from which the genus is known it is rare or infrequent. Few fossil deposits have been studied in such detail that we have an adequate knowledge of their floristic content. Although fossil deposits exposed on land have been studied for more than a century, there has until recently been a strong bias against detecting the smaller species present. These were discarded when samples were being prepared in such a way as to provide specimens not even partially obscured by broken fragments, e.g. when samples were sieved. It is only in recent years that this has not been normal practice. In spite of the comparatively intensive study of the Paleocene and Eocene deposits of the Volga basin in Russia during the late nineteenth and early twentieth centuries, the presence of small species of *Rutilaria* in these was not known until their discovery by Anisimova was reported (Proshkina-Lavrenko et al., 1949). Dr F. Hustedt later retained the small specimens when preparing material of Paleocene age from Inza, Ulyanovsk oblast, Russia. In this material there are four small species of *Rutilaria*, described below as *R. minima* R. Ross, *R. delicatula* R. Ross, *R. hyalina* R. Ross and *R. hustedtii* R. Ross. Three of these species are no doubt those recognized by Anisimova, but all of them were otherwise previously unknown.

The fossil diatomite of late Eocene to early Oligocene age from Oamaru, New Zealand, has been even more comprehensively studied than the deposits from the Volga basin. Nevertheless, a small species of *Rutilaria*, *R. areolata* Sheshukova-Poretskaya, is first reported from Oamaru in this monograph. Specimens of each of the two subspecies of this species are present on microscope slides, now in BM, prepared by H.-J. Schrader when studying the pennate diatoms of the Oamaru diatomite (Schrader, 1969). Because of the small size of many pennate diatoms, he had not discarded the small specimens in the samples that he studied.

The study of diatom biostratigraphy began about thirty years ago at the time when core samples from the ocean floor began to be available. Since then, the smaller diatoms have not been discarded. Nevertheless, specimens of *Rutilaria* present in samples examined in these studies are likely to have gone undetected. Biostratigraphers are primarily interested in those species that are frequent in the material that they are studying. Accordingly, they normally examine only two or three strewn slides from each sample, and often ignore the species that are rare on these. *Rutilaria*, however, is infrequent or rare in all the fossil samples in which it has been found and, although present in the material studied, might well not occur in the portion examined. The results of a study undertaken by Doig (reported in Edwards, 1991) show this. In order to compare the diatom assemblages in 40 different outcrops of the Oamaru diatomite, he identified and counted

300–500 specimens from each outcrop, 14 980 specimens in all. Amongst these less than 100 of the over 600 species known to occur in the Oamaru diatomite were represented, and there were only two specimens of *Rutilaria*, both of the same species identified by him as *Syndetoneis amplectans*. In this monograph there are records of nine species of the genus from the Oamaru diatomite.

Rutilaria is a neritic genus, and fossil deposits of diatoms laid down in shallow water are much more diverse floristically than those from deep sea localities. To find specimens of the genus in fossil deposits laid down in shallow water, whether ones already available but not intensively studied or ones newly discovered, will require prolonged searching. If this is done, it will undoubtedly extend our knowledge of the geographical distribution and the range in age of the species of *Rutilaria* already known and will also reveal the existence of others not yet described.

SOURCES OF SPECIMENS

In the course of preparing this monograph specimens from the localities listed below have been examined. They are arranged in a rather irregular sequence from west to east, beginning in western Europe. Most of the sources of material are fossil deposits and their age is given as precisely as the available information allows. Whilst the provenance of samples collected in the recent past is usually known exactly, the amount of detail available for some of those collected longer ago is often less adequate. In particular, there is often doubt about their precise geological age. Where this is so, the range of ages within which they might have been deposited is indicated in the form 'middle Eocene–Oligocene'. When the sample from which a specimen comes is known to date from very close to the boundary between one period and another but there is doubt about which side of that boundary it comes from, the age is given as, e.g., 'late Eocene to early Oligocene'. A number of the locality records given in the taxonomic account are based solely on the literature. For the most part all the information about the provenance of the specimens on which they are based is contained in the publication cited; where additional information is available it is given below.

Portugal

Redondo, Alto Alentejo Province

There is a strewn slide (BM coll. Adams J5185) labelled as from this locality. It came from the collection of F.B. Taylor and had been sold by Messrs C. Baker of London. Taylor (1929: 158) includes this locality in his list of the 'most interesting localities' for diatoms, but there is no other record of diatoms from there. The floristic composition is very similar to that of the upper Miocene material from Malaga Cove, Los Angeles County, California, U.S.A., often said to be from Redondo Beach or San Redondo, Los Angeles County, California, U.S.A. (see p. 7 below). It is thus highly likely that 'Redondo, Alentejo' on the label of this slide is an error for the Californian locality.

France

St. Laurent-la-Vernède, Gard

Details of the fossil deposit at this locality are given by Lefébure (1935) and Monjanel (1987), who dates it as early Miocene.

Denmark

Knudeklint, Island of Fur

Specimens of *Rutilaria* were found in portions of samples D 292 and D 294 from this locality kindly sent me by Dr M. Homann. These samples come from near the Paleocene to Eocene boundary. For details see Homann (1991).

Slovakia

Pôtor (Szent Péter), Banská Bystrica region

According to Hajós (1986: 162, 165), this deposit is lower middle Miocene, as also is the deposit from Velky Krtis (Nagykürtös) from which Pantocsek (1889) records *Rutilaria philippinarum* and *R. szakalensis*.

Hungary

'Castel', Szurdokpüspöki

Chenevière distributed fossil material labelled as coming from 'Castel'. The diatom flora that it contains shows that it is the material which is the subject of Chenevière's (1933, 1934a) account of diatoms from 'un dépôt nouvellement découvert près de Szurdokpüspöki, au voisinage du château', a deposit that he dated as late Miocene. This dating is, however, open to question. Holmes & Brigger (1979) give in translation an extract from a letter from Chenevière to Brigger written in 1938 in which he says of this material: 'this earth is very difficult to obtain; the outcrop is no greater than 1 m²!! and it is the only marine part in the middle of a very large freshwater deposit; its presence is incomprehensible.' This indicates that this marine diatomaceous earth is a block of older material that is not in situ but had become detached, transported into a body of fresh water and incorporated into the sediments forming there. If this is the case, it is older than the freshwater deposit in which it occurs. According to Hajós (1986: 169–171) this is of middle Miocene (Badenian) age. One cannot tell how much older the 'Castel' marine material is, but its floristic content indicates that it is Neogene rather than Paleogene. Marine diatomaceous deposits from the lower Miocene and from earlier in the middle Miocene are known from a number of localities some 50 km north of Szurdokpüspöki (Hajós, 1986), i.e. from higher in the valley of the river Gyöngyös, and this area would seem to be the most likely source of the 'Castel' material. Its diatom flora does, however, include a number of species that have not been found in any other locality. There can thus be no certainty about either where it came from or its precise age. It cannot, however, be younger than the middle Miocene, and specimens from it are listed as being of that age, although they may be older.

Szurdokpüspöki

There is a specimen of *Rutilaria* in CAS which came from material collected by Hajós in 1960 which is labelled as coming from Szurdokpüspöki and as being of Tortonian, i.e. late Miocene, age. This presumably came from the upper marine diatomaceous beds exposed in the diatomite quarry at Szurdokpüspöki, which Hajós (1986: 171) now dates as Badenian, i.e. middle Miocene.

Nógrádszakál

According to Hajós (1986: 179–182), the deposit at Nógrádszakál (Szakal of Pantocsek, 1886, 1889) is late middle Miocene in age.

Ukraine

Dneiper – Dombas depression

A micrograph of a specimen with the information that it came from late Eocene material from this area was sent me by Dr A. Ol'shtynskaya.

Russia

Kantemirovka, Voronezh oblast

Photomicrographs of a specimen of *Rutilaria grevilleana* from the late Eocene deposit at this locality were sent me by Dr Strel'nikova. She misidentified this as *R. limoniformis* (Strel'nikova, 1987).

Voronezh anticline, Voronezh oblast

A micrograph of a specimen from the late Eocene of this area was sent me by Dr A. Ol'shtynskaya.

Sengilei, Ulyanovsk oblast

Probably early Eocene but possibly Paleocene (see Ross & Sims, 1985: 280).

Inza, Ulyanovsk oblast

Paleocene (see Glezer in Glezer et al., 1974: 110)

Kuznetsk, Penza oblast

According to Glezer (in Glezer et al., 1974: 135), the fossil material from this locality studied by Pantocsek and other late nineteenth and early twentieth century diatomists is late Eocene in age. However, according to Dr J.A. Barron (in litt., 1994), the late Eocene dates assigned to some deposits by Russian diatomists were based on incorrect information about the age of formations in California and Barbados and the deposits in question are older. He kindly examined a sample of the classic fossil material from Kuznetsk and found that it was from the early middle Eocene.

'Kamischev', presumed to be Kamyshlov, Sverdlovsk oblast

Chenevière (1934*b*) gave an account of the diatoms of a fossil deposit that came, he said, from 'Kamischev', and he distributed material of this deposit. However, the actual locality from which it came is uncertain. Both Glezer (in Glezer et al., 1974: 136) and I (Ross, 1972) independently came to the conclusion that it came from Kamyshlov in Sverdlovsk oblast. Both Jousé (1955) and Glezer date the material from there as late Eocene. However, Dr Barron kindly examined a sample of the material distributed by Chenevière and reported (in litt., 1994) that its age is early Eocene. This too appears to be the age of Jousé's material from Kamyshlov, and it seems reasonable to assume that the deposit from Irbit studied by Krotov and Shibkova (1959) is also early Eocene.

Til'tim, Tyumen'sk oblast

Campanian, late Cretaceous. Exposure XI/14, sample 14, for which see Strel'nikova (1974), is the sample indicated, probably erroneously (see p. 000) as the source of a specimen of *Rutilaria*.

Coast of Arabia

Recent material not more precisely localized.

Tanzania

Zanzibar

Recent material.

Indian Ocean

Mascarene Ridge, 10° 25'S, 63° 15'E, 3115 m depth, dredge sample. Dodo-123-D1

This sample is from the boundary between the middle and the upper Eocene (see Holmes & Brigger, 1979).

Ninety East Ridge, 11° 20.21'S, 88° 43.08'E, 1655 m depth. Deep Sea Drilling Project Hole 214, core 38, section 2, 100–102 cm.

This sample is from the Paleocene (see Shipboard Scientific Party, 1974).

Indonesia, Java

Goenong Gamping, near Nanggoelang, sample AY-12

This sample is from the middle Miocene (see Reinhold, 1937: 57, 58).

Road from Mantoep to Pelang, Station 109M, Java Kaarteering-Sheet 109D (Lamongan) no. 83

This sample is from the East Java Horizon, Poetjangan layer, which is late Pliocene in age (see Reinhold, 1937: 57, 59, 67).

North side of mountain near Boetak. sample BS–8, *Pithecanthropus* skull sample of Prof. Dubois

This sample is from the middle Pleistocene (see Oakley et al., 1975: 113–114).

Indonesia, Makassar Strait

Recent material.

Indonesia, Sulawesi

Recent material.

Philippine Islands

Recent material not more precisely localized.

Jolo, Sulu Archipelago

Recent material.

Mindoro Strait

Recent material.

Manila

Recent material.

Chinese canned fish

For the provenance of this recent material see Fuge (1937).

Japan

Specimens with a locality no more precise than this were all mounted in the nineteenth century. They may be Miocene or early Pliocene in age.

Japan, Honshu

Tokyo-wan

The material from this locality studied by Brun & Tempère (1889) consisted of pebbles dredged from the sea bed. This material is Miocene but its age within that epoch and the locality of the outcrop from which it came are unknown.

Sendai, Miyagi Prefecture

Brun & Tempère (1889) say of the sample from this locality: 'Ce calcaire … constitue des cailloux roulés de grosseurs très variables.' This material was thus not in situ when it was collected and the locality of the outcrop from which it came is unknown. Akiba (1987) showed that it is late Miocene in age.

Ajigasawa, Aomori Prefecture

The details of the sample from this locality are: Maido formation, near Ajigasawa station, Ajigasawa, Maido-mura, Nishi-tsugaru-gun, Aomori Prefecture, Japan, coll. T. Kanaya, 1948. According to Akiba (in litt., 1991) the Maido formation extends from the upper Miocene into the Pliocene.

Sado-shima Island

Two specimens of *Rutilaria* come from this island, with no more precise information about the locality from which they came. The most probable source is the Sawane deposit at 37° 59′ 40″N, 138° 15′ 50″E (cf. Okuno, 1952). According to Akiba (in litt., 1991), this material probably comes from the Nakayama formation, which ranges from the late Miocene to the very early Pliocene (see Akiba, 1987).

Japan, Hokkaido

Specimens from this island not more precisely localized, including those labelled 'North Japan', come from one or other of the Miocene or early Pliocene diatomite deposits that occur there.

Hakodate, Oshima

Miocene or early Pliocene, but no more precise details are available.

Netanai, Oshima

The material so labelled is presumably from the Neogene Shirikishinai deposit that outcrops at Netanai (see Okuno, 1952). It is probably Miocene.

Setana, Miyama

Probably from the Kuromatsunai formation that extends from the upper Miocene to the lower Pliocene (Akiba in litt., 1991). The specimens of *Rutilaria* from this locality do not come from the freshwater deposit mentioned by Okuno (1952: 5).

Abashiri, Abashiri

There are both Miocene and Pliocene deposits at this locality. According to Kanaya (1959), the material from here is probably early Pliocene in age, but Akiba (in litt., 1991) thinks the flora recorded from there indicates that the classic 'Abashiri deposit' is middle Miocene, and this age is accepted here.

Tokoro, Abashiri

Akiba (in litt., 1991) says that an upper Miocene deposit containing diatoms occurs at this locality.

Embetsu, Rumoi ('Wembets' of Tempère & Peragallo, 1893, 1912)

According to Okuno (1952), this deposit is early Pliocene, but Akiba (in litt., 1991) says that there are both late Miocene and Pliocene deposits at this locality.

Teshio, Rumoi ('Thesiogori' and 'Theshiogori' of Pantocsek, 1892, 1905)

Akiba (in litt., 1991) says that there are both late Miocene and Pliocene deposits at this locality.

Bering Sea

Komandorsky Islands, Russia

The fossil deposits from these islands have been studied by Gladenkov (1991). Their ages range from early Oligocene to late Oligocene. The records from this locality are based on photomicrographs and samples that he kindly sent me.

Aleutian Basin, 54° 47′ 20″N, 179° 08′ 00″W, 1670 m depth. U.S.S. Albatross Station 4029H

Hanna (1929) showed that this sample is as old at least as the middle Miocene. *Kisseleviella carina* is moderately frequent in this material. This suggests that it comes from the lower Miocene or the lower part of the middle Miocene (see Akiba, 1985, and Akiba & Yanagisawa, 1985). Specimens from this locality are therefore listed as having an early Miocene age.

Navarin Basin, 56° 12.3′N, 171° 42.2′W, 2500–2700 m depth. U.S. Geological Survey Research Vessel S.P. Lee, cruise L5-78-BS, dredge sample 2-4

This sample is from the upper Oligocene (Baldauf & Barron, 1987).

U.S.A., Oregon

Coos Bay, Coos County. California Academy of Sciences sample 1612

This sample is from the upper Eocene Bassendorf Shale exposed at the south end of Coos Bay.

U.S.A., California

Specimens with no more precise locality are from gatherings made in the nineteenth century and come from one or other of the middle Miocene to lower Pliocene diatomite deposits exposed in the coastal region of California from San Francisco southwards.

Antioch, Contra Costa County

The details of the sample from here are: Contra Costa County, NE 1/4, Sec. 2, T.1N., R.1E, M.D.M. 2½ miles S of Antioch. The geographical co-ordinates of this locality are 121° 49′ 49″W, 37° 57′ 48″N. Its diatom flora was described by Hanna (1931), who regarded it as coming from the Kreyenhagen Shale of late Eocene age (Jenkins, 1931). It is the type locality of the 'Sydney' shale of Clark & Campbell (1942); see also Kanaya (1957) and Mandra (1968). According to McLean & Barron (1988) this is late middle Eocene, being in Barron's informal *Triceratium inconspicuum* var. *trilobatum* partial range zone.

Laguna Seca Creek, Merced County

From 14 miles south of Los Banos at abandoned mine, from cuts near top of section near abandoned process plant, Kreyenhagen shale. This is the Oro Loma locality of McLean & Barron (1988), also in the late middle Eocene *Triceratium inconspicuum* var. *trilobatum* partial range zone.

Panoche Road, Panoche Hills, Fresno County

Mined earth from the upper Eocene Kreyenhagen Shale.

Cantua Creek, Fresno County

The details of the sample from this locality are: 1/4 sec. 28, T17S R14E, 200–300 feet below top of Lillis Shale. The age of the material is thus late Eocene (see Jenkins, 1931).

Salinas, Monterey County

Upper Miocene. Diatomaceous material from this locality is of the same age as that from Monterey (see Hanna, 1928a: 975).

Monterey, Monterey county

The samples said to come from Monterey almost certainly come from the outcrop of the Monterey Shale four miles east of Monterey, the locality of the type Delmontian Stage. According to Hanna (1928a), this dates from about the boundary between the middle and the late Miocene, probably from the earliest late Miocene. Wornardt (1967: 7), however, says that the Monterey diatom flora is from the top of the upper Miocene and that the same diatom assemblage occurs elsewhere in California. More recently Barron (1976a) has shown that Hanna's is the correct date.

'Santa Lucia'

Specimens said to be from this locality presumably come from one of the numerous deposits of Miocene diatoms that outcrop on the inner, eastern side of the Santa Lucia Mountains, Monterey County (see Hanna, 1936). According to Wornardt (1967) these are late Miocene in age, but Barron (in litt., 1991) says that upper middle Miocene diatomaceous rocks are more common in this area, although samples from there could be upper Miocene.

Santa Maria, Santa Barbara County

One cannot be certain whether the material collected in the nineteenth century and labelled as from Santa Maria, California, came from the lower upper Miocene Monterey formation or the uppermost Miocene to lower Pliocene Sisquoc formation (for the age of this see Barron & Baldauf, 1986), both of which are exposed in the Santa Maria district (Woodring & Bramlette, 1950). The Sisquoc formation is, however, more widely and more accessibly exposed there and is thus the more likely source.

Paradise Cove, Malibu, Los Angeles County

Malibu, Los Angeles County

Specimens labelled as from Malibu presumably come from the outcrop of Miocene material at Paradise Cove. The most likely age for this is early in the late Miocene (Barron in litt., 1991).

Temescal Canyon, Santa Monica, Los Angeles County

Barron (in litt., 1991) has found late Miocene diatoms from this locality.

Malaga Cove, Los Angeles County

The outcrop of upper Miocene diatomiferous rock at Malaga Cove is the source of the 'floating fossil', a block of diatomite found on the beach at Santa Monica, Los Angeles County; it is also the nearest outcrop to Redondo Beach (San Redondo), which is four miles to its north-west (Hanna, 1928b, 1936; Laporte, 1936). Specimens labelled as from Santa Monica, Redondo Beach, or San Redondo are all from this outcrop. Both the diatomite-rich upper Miocene Valmonte Diatomite and the uppermost Miocene to lower Pliocene more mud-rich Malaga Mudstone are exposed at Malaga Cove (Barron in litt., 1991), but the samples studied by diatomists almost certainly all came from the Valmonte Diatomite.

Los Angeles, Los Angeles County

The upper Miocene Valmonte Diatomite has extensive outcrops in the suburbs of Los Angeles, not only at Malaga Cove but also in the area of the Palos Verdes Hills and San Pedro. The specimen with no more precise locality than Los Angeles, and those from any of the following three localities almost certainly came from this formation (Barron in litt., 1991):

Palos Verdes, Los Angeles County
Channel Road, San Pedro, Los Angeles County
San Pedro, Los Angeles County

Newport Beach, Orange County

Specimens labelled as coming from Route 101, Newport, as well as those labelled only Newport or Newport Beach, come from the middle and upper Miocene Monterey formation exposed there (see Barron, 1975, 1976b).

Mexico

Maria Madre Island

Samples of diatomite of high purity were obtained from the bank of the Arroyo Hondo, about 2–3 miles inland from the north coast of this island (see Hanna & Grant, 1926). The material is late Miocene (see McCloy et al., 1988).

New Zealand

Oamaru, Otago

Edwards (1991) gives detailed descriptions of all the known outcrops of the Oamaru diatomite and diagrams of the stratigraphic columns at these localities. He shows that almost all the diatomaceous rocks are late Eocene in age, but that the uppermost ones exposed at Forrester's Hill and at Mavor's Farm are from the earliest part of the Oligocene. Long before the publication of this account of the Oamaru diatomite, Edwards assigned code numbers to each bed at each locality, prefixing these with letters indicating the locality, and Doig (1967) indicates how these relate to the names for outcrops used by earlier diatomists. The following is a list of the names of the outcrops from which specimens of *Rutilaria* are recorded together with the code designation as given by Edwards (1991):

Allan's Farm = AF3
Bain's Farm = BN7(3), BN9(3)
Bain's Farm, lower = BN9(3)
Borrie's = PP (one or more unspecified outcrops with this prefix)
Cave Valley = CS1 according to Edwards (1991: 57)
Cormack's Siding = CS1
Dick's Farm ?= Jackson's Well, but see Edwards (1991: 53)
Flume Creek = Flume Gully
Flume Gully = PP (any)
Forrester's Hill = FH2 or FH4. These two outcrops are just above and just below the Eocene to Oligocene boundary
Jackson's Farm = Jackson's Paddock
Jackson's Hill = JP3
Jackson's Paddock = JP3 (but a few specimens so labelled may be from JP5)
Jackson's Well (locality uncertain, see Edwards (1991: 53)
Lower Papakaiyo = PP12(N) (but a few specimens so labelled may be from PP10(N))
Mataura
Papakaiyo = PP8(N), PP10(N), PP12(N)
Railway Cutting = CS1, or perhaps CE3 or CE5
Totara = BN5(4)
Troublesome Gully = TG2, or possibly TG1
Williams' Bluff = WB1

All of these exposures, except FH2, are late Eocene in age. There are many specimens without any more precise locality than 'Oamaru'. These include specimens in Grove's and Sturt's collections that were from the original sample on which their account of the diatom flora of the Oamaru diatomite was based. According to Lautour (1889), this came from the outcrop CS1. It is very unlikely that any of the specimens labelled simply 'Oamaru' came from the uppermost diatomites at Forrester's Hill or Mavor's Farm, which are the only ones above the Eocene to Oligocene boundary. These specimens are therefore listed as late Eocene. In the distribution records for the individual species, the outcrop, when this is indicated, is given as on the label of the specimen. The list above shows which of the beds delimited by Edwards (1991) are referred to by these outcrop names.

South Atlantic

Falkland Plateau, Vema cruise 12, core 46, 47° 28.7'S, 59° 20.6'W, depth 1167 m, 630 cm from top of core

Middle Eocene with a strong admixture of Paleocene and early Eocene (Fenner in litt., 1984).

Falkland Plateau, Vema cruise 17, core 107, 51° 08'S, 54° 22'W, 1525 m depth, 50 cm, 120 cm, and 175 cm from top of core

All middle Eocene (Fenner in litt., 1984).

Falkland Plateau, Vema cruise 18, core 104, 53° 01'S, 52° 52'W, 2880 m depth, 330–333 cm from top of core

Middle to late Eocene (Fenner in litt., 1984).

Falkland Plateau, Vema cruise 18, core 112, 51° 40'S, 48° 29'W, 2429 m depth, 100 cm from top of core

Lower Oligocene (Fenner in litt., 1984).

Falkland Plateau, Conrad cruise 12, core 237, 47° 45.7'S, 57° 38.5'W, 3650 m depth

Eocene, probably middle or late, rather than early, Eocene.

Barbados

The fossil diatoms from this island occur in the Oceanic Beds, which range in age from the middle Eocene to the early Miocene. Specimens of *Rutilaria* with a locality no more precise than 'Barbados' may have come from any age within this range. However, the only samples containing diatoms that have been dated as Miocene are from Conset Bay, and the species present in samples from other localities that have not been firmly dated suggest that none of these are older than the Oligocene. It seems probable that this is also the case for specimens with the locality given as nothing more than 'Barbados'. All such specimens are therefore regarded as coming from within the range middle Eocene–Oligocene.

Cambridge Estate

All the specimens from this locality come from material distributed by C. Johnson in the middle of last century. The Radiolaria on two strewn slides of this material indicate that its age is middle Eocene (Riedel in Holmes & Brigger, 1979). There is uncertainty about the locality from which this material came (see Robinson, 1941b).

Chimborazo

Brun (1896) had material from this locality, and there are specimens from it mounted by Brigger at BM and CAS, but there is no information about the site from which it came nor about its precise age.

Clealand

Brun (1896) records a specimen from this locality, but there is no further information available about its provenance.

Conset

A sample from Conset collected by J.H. Robinson was sent by Holmes & Brigger (1979) to W.R. Reidel, who dated it as early middle Eocene on the basis of the Radiolaria it contained. Robinson (1936) gives details of two localities in Conset from which he had obtained samples containing diatoms. Robinson and F.W. Adams collected in Barbados early in 1936 (Robinson, 1937) and obtained further samples from the Conset area. There are strewn slides prepared from these samples and mounted by F.W. Adams in his collection now in BM. Dr J.A. Barron of the U.S. Geological Survey has kindly examined these for me and gives the following ages for them:

Manjack Hole, Conset Bay; middle Eocene
College Hill, Conset Bay; early Oligocene
Burnt Hill, Conset Bay; early Oligocene
St Mark's, Conset Bay; late early Miocene

Railway Track, Conset Bay; late early Miocene

The only specimen of *Rutilaria* on these slides is one of *R. elliptica* Greville from Burnt Hill. In addition Brigger mounted many specimens from these samples, but gave only Conset as their locality; they may have come from any one of the samples from there. It would seem that he assumed that these samples did not need to be distinguished from one another. These specimens include all the known specimens of *Rutilaria flabellifera* R. Ross and the only specimen of *R. szakalensis* Pantocsek from Barbados. The sample sent to Riedel presumably came from Manjack Hole. It seems reasonable to assume that species known elsewhere only from the Miocene and recorded from Conset but nowhere else in Barbados come from one of the lower Miocene samples. Examples are *Rutilaria szakalensis*, *Briggera haitensis*, *Entogonia formosa* and *E. jeremiana*. *Rutilaria flabellifera* also has not been found elsewhere on Barbados. There is little doubt that it is an evolutionary successor of the middle Eocene *R. cantabrigiensis*, and that it therefore comes from an early Oligocene or an early Miocene sample rather than a middle Eocene one.

Joe's River

All the specimens from this locality come from material distributed by J.H. Robinson, who gives details of the site from which it came (Robinson, 1938). According to Riedel, the Radiolaria in this material indicate that it comes from the upper Eocene to Oligocene boundary (Holmes & Brigger, 1979).

Mount Hillaby

No details about the precise site or age of the diatomite from this locality are available.

Springfield

Robinson (1941a) gives details of the site of the quarry that is the source of the diatomite from this locality, and also a list of species found there. This list suggests that the most probable age for this deposit is late Eocene. It is probable, but not certain, that the nineteenth century samples from Springfield came from the same quarry as Robinson's material and specimens from there have accordingly been considered to be of late Eocene age.

Haiti

Jérémie

Truan & Witt (1888) give details of the source of the fossil material from this locality. A sample of this was dated by Riedel as early Miocene on the basis of its Radiolaria (Holmes & Brigger, 1979). Ross & Sims (1985: 284) expressed doubts about this dating, but now that it is known that some samples from Conset Bay, Barbados, are early Miocene in age (see above) there is no longer any reason to question its accuracy.

Gonaïves

There are specimens from fossil material from this locality in Brun's collection at G, but no details about the precise site or about the age are available. The specimens include one of *Rutilaria grevilleana* subsp. *monocellata*, otherwise known only from the lower Eocene of the Blake Plateau, North Atlantic, and one of *R. amplectans*, otherwise known from material from the middle to upper Eocene boundary in the Indian Ocean and from the upper Eocene of Oamaru, New Zealand. An Eocene age is therefore assumed for these diatoms.

North Atlantic

Blake Plateau, 30° 08.54′N, 76° 06.74′W, 2665 m depth, Deep Sea Drilling Project Hole 390A, core 7, section 4, 129–131 cm

This sample is from the lower Eocene (see Gombos, 1982).

Bermuda Rise, 30° 53.39′N, 67° 38.86′W, 5125 m depth, Deep Sea Drilling Project Hole 6

The specimens from this locality, including those examined with the scanning electron microscope, were all selected by A.L. Brigger. He had samples from core 3–4, 72–78 cm down to core 6–3, 20–24 cm. All the material throughout this range is middle Eocene in age (Berggren, 1969: 606).

Labrador Sea, 53° 19.876′N, 45° 15.717′W, 3870 m depth, Ocean Drilling Programme Hole 647A, core 19R, section 1, 125–127 cm

This sample is from the lower Oligocene (Monjanel, 1987).

TAXONOMIC ACCOUNT

The terminology used in the descriptions of the genus and the species is that given in Anonymous (1975) and Ross et al. (1979), with a few additions and one modification. 'Projection', 'interrupted striae' and 'sibling valve' are used in the sense defined by Ross & Sims (1985). 'Marginal spine' and 'superficial spine' are used in the sense defined by Ross (1990). The marginal spines are usually slightly inset from the margin of the valve face and form two rows, one along each margin, that are separate throughout. In some species with very narrow projections, however, the two rows, one on either side of the central portion of the valve and the proximal parts of the projections, meet and continue as a single row along the centre of the distal parts of the projections (see, e.g.,Plate VIII (e)). These spines on the mid-line of the distal parts of the projections are nevertheless also called marginal spines as they need to be distinguished from the superficial spines that occur in some species sparsely scattered on the central portion of the valve and the proximal parts of the projections. A structure peculiar to *Rutilaria* is the periplekton, a modified labiate process consisting of a vertical tube, the stem (*caulis*), from the top of which two arms (*brachia*) project horizontally and encircle the stem of the periplekton of the sibling valve, forming a ring (*annulus*) (see Plate 2 (d)). In a number of species there is a flange

(*margo alata*) along the outer side of the arms that form the ring of the periplekton (see, e.g., Plate XII (b)). The length of the pervalvar axis, i.e. the depth of the frustule, is considered to be the distance between the bases of the periplekta of the two valves; the periplekta, and the elevations present at the apices of many species, are not included.

Round, Crawford & Mann (1990: 48–49) have criticized the terminology for the girdle bands proposed by von Stosch (1975) and adopted in Anonymous (1975) and Ross et al. (1979). They point out that there is no general criterion for distinguishing between copulae and pleurae as defined by von Stosch and that the change in the morphology of the girdle bands between the more advalvar and the more abvalvar is often gradual, not abrupt. They therefore suggest that all girdle bands be termed copulae, the one immediately adjacent to the valve, which usually differs somewhat from the others, being called the valvocopula, the others being numbered in abvalvar sequence. This suggestion is followed here and the girdle bands are referred to as valvocopula, copula II, copula III, etc. Most of the descriptions of the girdles are incomplete. Almost all the species of *Rutilaria* are fossil and in fossil material complete girdles attached to valves are infrequent to rare. Also, specimens of bipolar species mounted in girdle view for light microscopy almost invariably lie with the apical axis parallel to the slide on which they are mounted. When specimens are in this position, it is often impossible to see whether copulae are open or closed. This can be seen on scanning electron micrographs but very few of these showing specimens with intact girdles have been available.

Five species are divided into two infraspecific taxa and these are given the rank of subspecies. The differences in morphology between the two subspecies of one species are very slight, appreciably less than those between the taxa that are recognized as distinct species. In four cases the two subspecies do not occur in the same fossil deposits. In two of these, *Rutilaria hannai* R. Ross and *R. tenuicornis* Grunow, the two subspecies are separated not only geographically but also in time; they do not occur in the same geological period. There may also be a slight difference in age between the fossil deposit at Inza, Russia, and the Danish Fur formation in which the two subspecies of *R. minima* R. Ross have been found. The two subspecies of *R. grevilleana* (Walker & Chase) R. Ross are both present in the early Eocene but their known occurrences at that time are well separated geographically. The length of time during which both were present is, however, uncertain as the age of one of the two deposits in which *R. grevilleana* subsp. *monocellata* R. Ross has been found, that at Gonaïves in Haiti, is not known. Both subspecies of *R. areolata* Sheshukova-Poretskaya occur together in the late Eocene of Oamaru, New Zealand, but their other records are from different localities and these may not overlap in time. Diatomists have, for the most part, used the rank of variety for infraspecific taxa, but most of those recognized have been taxa similar in kind to the phenodemes found in *Sellaphora pupula* (Kützing) Mereschkowsky (*Navicula pupula* Kützing) and described by Mann (1984). These clearly have a different status from the infraspecific taxa recognized here, which seem to be comparable with those treated as subspecies in higher plants by those authors who recognize infraspecific taxa of that rank (cf. Hamilton & Reichard, 1992).

In the synonymies for each species and subspecies all the accounts of the taxon that are accompanied by illustrations

are cited. An appreciable number of records are shown by the figures that accompany them to be based on misidentifications. In consequence there are very few records not accompanied by figures on which one can rely, and only these few are included in the synonymies and the distributions. A few published figures are not detailed enough for certainty as to the identity of the specimen shown. References to accounts accompanied by such illustrations are given under the taxon to which they probably refer preceded by a question mark ('?').

Drawings of each taxon, as well as photomicrographs and, where available, scanning electron micrographs, are provided. Because the depth of focus obtainable with the light microscope is so limited, a photomicrograph cannot show all the morphological detail needed to distinguish a taxon, whereas a drawing can. With one exception, the scanning electron micrographs reproduced here were taken in BM and are preserved in the collection there. Their reference numbers are given in the explanations of the figures.

The herbarium or institution in which the holotype of a new taxon is conserved is indicated by the acronyms given in *Index herbariorum* (Holmgren, Holmgren & Barnett, 1990) and also by Fryxell (1975). A number of the holotypes conserved in BM are on strewn slides or selected slides with many species present. When this is the case the citation of this slide is preceded by 'in'. The position of the holotype specimen on the slide is given in the documentation of the diatom collection in BM.

In the distributions given for each species or subspecies, all the specimens that I have seen are listed, apart from the very few which are not localized. In these lists also the institutions in which the specimens are conserved are indicated by the acronyms given in *Index herbariorum*. In addition, the scanning electron micrographs taken and preserved in BM are listed. With a few exceptions, records from the literature are given only when they are from a locality from which no specimens have been seen. The few records attributed to 'personal communication' are based on unpublished micrographs kindly sent me by colleagues. The records are arranged according to the geological age of the material in which the specimens occurred and, within any one geological period, in the geographical order adopted in the section on the sources of specimens (pp. 3–9 above), where fuller details about each locality are given, including the evidence on which specimens from there have been assigned to a particular geological period. Where there is doubt about the geological age of material from which specimens come, the range of age within which it might have been deposited is given in the form 'middle Eocene–Oligocene'; where it is known to come from very close to the boundary between two periods, its age is given as, e.g., 'late Eocene to early Oligocene'. As mentioned above, records that are probable but not certain because they are based on inadequate illustrations are preceded by a question mark. In some cases I believe that the locality given on the label of a specimen is an error; such records are enclosed in square brackets ('[ ]').

The order of the species in this account is such as to bring together those that seem most closely related, and those in each group are arranged in the order of their appearance in the fossil record, with one exception. It was not until this paper was reviewed by Dr J.A. Barron that I learnt that the date attributed by Jousé (1955) and Glezer (in Glezer et al., 1974) to the deposit at Kamyshlov was incorrect. By that stage all the figures had been prepared for publication and it

was not possible to move the account of *Rutilaria kamyshlov-ensis* R. Ross so that it preceded that of *R. interrupta* R. Ross instead of following that of *R. hannai* R. Ross.

RUTILARIA Greville in *Q. Jl microsc. Sci.*, new ser. **3**: 227 (1863).

Syndetocystis Ralfs ex Greville in *Trans. microsc. Soc. Lond.*, new ser. **14**: 125 (1866).
Syndetoneis Grunow in *Bot. Zbl.* **34**: 36 (1888). – De Toni, *Syll. alg.* **2**: 1019 (1894).

Frustules united in inseparable short chains. Valves normally bipolar, circular, elliptical, broad lanceolate or sub-hexagonal, often with projections that may be long and subcapitate or capitate. Small apical elevations present in some species. A sub-circular to circular hyaline central area present, the rest of the valve areolate, the areolae poroid, in radial striae or irregularly arranged. In the centre of the valve a periplekton, a modified rimoportula, its internal opening a straight slit across a slightly raised papilla, its external part consisting of a vertical tube, the stem, with at its upper end two lateral arms that form a ring clasping the tube of the periplekton of the sibling valve. An ocellus without a thick-ened rim present at each pole on the distal face of the elevation or on the mantle. Marginal spines present in most species, sometimes with a gap opposite the central area, sometimes absent on the distal part of the projections, sometimes forming a single row along the centre of the distal part of narrow projections; occasionally two parallel rows of such spines along each margin of the valve, those in the outer row smaller and more closely spaced than those in the inner row. Scattered superficial spines sometimes present on the valve face. Cingulum consisting of two to five copulae, the valvocopula open or closed, the other copulae open.

LECTOTYPE SPECIES. *Rutilaria epsilon* Greville (see Round, Crawford & Mann, 1990: 314, 701).

Three species were included in *Rutilaria* when it was first described: *R. epsilon*, *R. elliptica* and *R. ventricosa*. *R. epsilon* was the earliest of these to come to Greville's attention, and his account of the genus is based more on this species than on the others; it is accordingly the most appro-priate choice for a lectotype. The first designation of a lectotype, however, was not made until 1990.

The generic name *Syndetoneis* first appeared in Grunow's (1888) comments on Grove and Sturt's account of the dia-toms in the deposit at Oamaru, New Zealand. He says of the species that they had called *Hemiaulus amplectans* Grove & Sturt (1887a: 76):

Syndetoneis amplectans (Gr. et St.) Grun. (Hemiaulus amplectans Gr. et St.) Sicher kein Hemiaulus. Verwandt mit Ditylium, aber Biddulphia-artig mit 2 hohen Polstern und dicker, oben getheilter Centralborste, die wie bei Syndetocystis die Borste der benachbarten Schale umschlingt. Bei Syndetocystis sind die Frusteln cylindrisch.

It is not easy to decide whether these remarks constitute a diagnosis of the genus *Syndetoneis*, giving it valid publication, or whether they refer to the species. They cannot be treated as a *descriptio generico-specifica* under Art. 42.1 of the *International code of botanical nomenclature* (Greuter et al.,

1994) as the previously published name *Hemiaulus amplec-tans* has the same type. However, as Grunow points out how the taxon differs from other genera, I here take the view that his remarks are to be regarded as a diagnosis of the genus and hence that the generic name *Syndetoneis* and the combination *S. amplectans* were validly published by him. Should the opposite view be taken, then those names were validly published by De Toni (1894), who attributed them to Grunow.

When *Rutilaria* was first described it was believed by Greville, and also by Kitton and Rylands, whom he con-sulted, that the specimens on which the genus was based were in front (girdle) view, whereas they were actually in valve view. As a result of this misapprehension the structure of the valve was completely misunderstood and the genus was thought to be related to *Nitzschia*, the marginal spines being equated with the keel puncta (fibulae) of that genus. In the next few years specimens in girdle view, and one at least lying obliquely, were found, and these enabled Greville (1866) to give a more accurate account of the genus, and to suggest that its affinity was with the Biddulphieae rather than with *Nitzs-chia*. He did not, however, give an accurate account of the periplekton but described it as 'a central glistening nodule prolonged into two short, linear, obtuse processes', adding that Rylands had 'satisfied himself that of the two central processes one was straight and the other curved as in the flexure of a forefinger; and that the processes of the opposing valves were interlocked, the straight process of the one passing mutually through the curved process of the other.'

The next attempt to describe the periplekton of *Rutilaria* was by Jurilj (1965), who introduced that term for the structure in the centre of the valves of that genus, *Syndetocys-tis* and *Syndetoneis*. Intervening authors referred to the periplekton as 'central peculiar nodule' (H.L. Smith, 1872: 15), 'nodulo centrali elevato convoluto vel tuberculiformi' (De Toni, 1894: 1021), 'a peculiar hooked central nodule' (Van Heurck, 1896: 429) or 'a peculiar central nodule pro-longed into two, short, linear, obtuse processes' (Van Heu-rck, 1896: 433), 'einem kurzen, knotenartigen, gewundenen oder höckeringen Forsatz, mit dem die Nachbarzellen verw-achsen' (Schütt, 1896: 100; Karsten, 1928: 250), or 'poro centrali processu convoluto vel bifurcato' (Forti, 1912). According to Jurilj (1965) the periplekton of *R. radiata* Grove & Sturt consists of an upright stem with, at its top, a circular loop that encircles the stem of the sibling periplek-ton. However, as can be seen from the illustration provided by Ross & Sims (1972: fig.30) and from Plate III (c), (d) of this paper, the ring of the periplekton in this species is formed by two arms whose tips overlap. This is true of all species of *Rutilaria* except for *R. flabellifera* R. Ross, which has no ring, and perhaps also *R. attenuata* R. Ross.

Until now, almost without exception, *Syndetocystis* Gre-ville and *Syndetoneis* Grunow have been regarded as genera separate from one another and from *Rutilaria*. Only one species has been included in each of these two genera, although both of these species have a number of synonyms. A detailed history of the inaccuracies in the figures and descrip-tions of *R. grevilleana* (Walker & Chase) R. Ross, the type species of *Syndetocystis*, is given under that species (pp. 14–17). Also, as is pointed out under *R. amplectans* (Grove & Sturt) R. Ross (p. 18), the type species of *Syndetoneis*, the accurate figure that accompanied its original publication has misled some authors into thinking that the periplekta of two sibling valves differed. For these reasons, it was not realized

that differences between the type species of the two genera were insufficient to support generic separation: presence or absence of marginal and superficial spines, size and arrangement of areolae, and height of elevations and periplekta. Grunow (1888) thought that the periplekta of the two genera were the same but that *Syndetocystis* had cylindrical frustules without elevations, whereas *Syndetoneis* had elevations. De Toni (1894), on the other hand, realized that both had valves with two elevations but maintained their separation on the basis of a supposed difference in their periplekta. He described that of *Syndetocystis* accurately as having a lateral ring at its summit, but said that in *Syndetoneis* the periplekta of sibling valves were dissimilar, one forked, one simple. The first author to combine the two genera was Lefébure (1947), who cited *Syndetoneis* as a synonym of *Syndetocystis* without comment. Jurilj (1965) tentatively suggested that the two genera should not be separated; according to him, *Syndetoneis* had a periplekton with a closed ring at its summit and *Syndetocystis*, which he knew only from literature, probably did so also. In this he was correct, except that the ring in both genera is not closed, as shown in his figures, but formed of two overlapping arms.

These mistaken views about the characters of *Syndetocystis* and *Syndetoneis*, combined with the ignorance of the structure of the periplekton of *Rutilaria*, prevented earlier authors from realizing that the three could not be separated at the generic level. Apart from an incidental mention by Ross & Sims (1973), this has not been pointed out until now. It had been realized much earlier, however, by Brun. In the Conservatoire Botanique de Genève there is a manuscript entitled 'Diatomées. Espèces et variétés nouvelles par J. Rataboul et J. Brun. Genève–Moissac. 1904. Projet de publication, arrêté par le mort du Mr Rataboul. J. Brun. 1905.' In this there is the following:

> Rutilaria Barbadensis Rt. & Br. olim. (Syndetocystis Barbadensis Ralfs.)
>   Cette figure qui représente la face valvaire est le complément de cette donnée par Ad. Schmidt et qui représente la face connective. Lire la notice du traité de Van Heurck (p. 432) et celle de Ad. Schmidt à la planche 173 de l'Atlas.
>   Avec leurs écailles sur la surface valvaire et leur fort épine axiale les Ditylum se rapproche aussi de Rutilaria. Cette espèce appartient en réalité aux Rutilaria dont elle a tous les caractères. La forme arrondie de sa valve ne permet guère d'en faire un genre à part, car certains types de ce genre ont une forme hexagone ou ovale, déjà plus ou moins arrondie. Voir le 'Diatom.' I 10/2 et II 5/19. 4492.

The figure referred to in this quotation was not with the manuscript, but 4492 is the number of a microscope slide in Brun's collection. This slide has on it selected specimens from Gonaïves, Haiti, including one of *R. grevilleana* subsp. *monocellata* R. Ross and one of *R. amplectans* (Grove & Sturt) R. Ross. The figure was presumably of the former.

It was over a century after *Rutilaria* was first described before it was pointed out that an ocellus was present at each pole of the valve. This fact was first mentioned by Simonsen (1972: 50), and an illustration showing one was provided by Ross & Sims (1973: fig. 50), although reproduction of this is so bad that it can scarcely be made out. As the figures in this paper show (e.g. Plate I (b), (f), Plate V (d), Plate VI (c), Plate XIX (d)), all the species that it has been possible to investigate with the scanning electron microscope, including

R. grevilleana and *R. amplectans*, have ocelli. As compared with the ocelli of such genera as *Auliscus* and *Eupodiscus*, those of *Rutilaria* are usually small and do not have a well developed rim. They are thus intermediate between the ocelli of these genera and the ocelluli of the Cymatosiraceae (Hasle, von Stosch & Syvertsen, 1983: 12).

A number of the species of *Rutilaria* are remarkable for their range of outline. The longest specimens of these species have capitate projections each of which is more than twice as long as the central portion of the valve, and there is a continuous gradation between these and specimens with elliptical, broad lanceolate or subhexagonal valves and no projections whatever. Most of these valves without projections are almost or quite as broad as those with long projections. *R. radiata* Grove & Sturt (see Fig. 19), *R. philippinarum* Cleve & Grove, *R. elliptica* Greville and *R. obesa* Cleve (see Fig. 76) all show such a range of outline, and there are indications that *R. interrupta* R. Ross and *R. hannai* R. Ross do so also, but not enough specimens of these species have been found for this to be certain. That there is such a wide continuous range of outline of specimens otherwise indistinguishable is only obvious when a considerable number have been seen. As a consequence, specimens from different parts of the range of outline of the same species have been regarded as belonging to separate species.

Rutilaria is a genus with a very long history. There is a record from the Campanian, but this is doubtful (see p. 32 below). It was certainly present in the Paleocene, and it has persisted until the present day. The two living species, *R. tenuicornis* Grunow and *R. philippinarum* Cleve & Grove, are both very uncommon members of the neritic plankton of tropical and sub-tropical seas. This seems to have been the habitat of the genus throughout its history, and its fossil representatives are never common in any of the deposits in which they occur. Some species have a long fossil history, the two living species the longest, from the middle Eocene to the present day. Others, however, occur through a very limited time interval and are also sufficiently frequent, although not common, to be of use for stratigraphic purposes.

KEY TO THE SPECIES

1. **Rutilaria grevilleana** (Walker & Chase) R. Ross, **comb. nov.**

Syndetocystis grevilleanus Walker & Chase, *Notes new & rare Diat.* **2**, **3**: 6, pl. 4 fig. 13 (1887) 'Grevilleanns'. – De Toni, *Syll. Alg.* **2**: 1019 (1894).

Syndetoneis sp. A. Schmidt, *Atlas Diatom.-Kunde*: Taf. 173 fig. 16 (1892). – Jurilj in *Acta bot. croat.* **24**: 74, fig. 5 (1965).

Syndetoneis russica Pantocsek, *Beitr. foss. Bacill. Ung.* **3**: Taf. 25 fig. 376 (1892); *Beschr. neu. Bacill.*: 103 (1905).

Syndetocystis russica (Pantocsek) De Toni, *Syll. alg.* **2**: 1019 (1894) 'rossica'. – Jurilj in *Acta bot. croat.* **24**: 74 (1965).

Syndetocystis barbadensis Ralfs in Van Heurck, *Treat. Diatom., transl. Baxter*: 432, fig. 155 (1896); *Traité Diatom.*: 432, fig. 155 (1899), nom. superfl. – Schütt in Engler & Prantl, *Nat. Pflanzenfam.* **1**(1b): 63, fig. 78 (1896). – Coupin, *Album crypt., Alg.* **5**: pl. 288 fig. G (1922). – Karsten in Engler & Prantl, *Nat. Pflanzenfam.*, 2 Aufl. **2**: 209, fig. 208 (1928). – Lefébure, *Atlas Déterm. Diatom.*: pl. 4 fig. 5 (1947). – Jurilj in *Acta bot. croat.* **24**: 73, fig. 8 (1965).

'N. S.' Laporte & Lefébure, *Diatom. rares cur.* **2**: pl. 17, fig. 114 (1930).

Coscinodiscus cladiscophorus Lefébure & Chenevière in *Bull. Soc. fr. Microsc.* **8**: 24, pl. 1 fig. 5, text-fig. 1 (1939).

Rutilaria lipica Ol'shtynskaya in *Paleont. Sb. Lemberg* **15**: 78, tabl. 1 fig 4 (1978).

Rutilaria limoniformis sensu Strel'nikova, *Paleogen. diatom. Vodor. vysok. Shirot Sever. Yuzhn. Polush.*: 8, 11 (1987), non R. Ross, 'lymoniformis'.

? *Rutilaria* sp. Fenner & Mikkelesen in *Proc. ocean drilling Progr., Sci. Rep.* **115**: 447 (1990).

Frustules with the pervalvar axis about equalling the apical axis. Valves sometimes slightly raised at the centre, with one or two elevations rounded in girdle view or sloping upward distally, 6–13 μm tall, elliptical in valve view and 10–15 μm long by *c.* 8 μm wide; valves 30–115 μm long, 24–95 μm wide, broadly elliptical or broadly lanceolate to circular Mantle separated from the valve face by a sharp angle, vertical, 4–6 μm deep, hyaline. Central area circular, ¼–⅓ of the breadth of the valve in diameter. Areolae large, *c.* 1.2 μm in diameter, occluded externally by domed vela perforated by one to three irregular holes or small slits, each velum bearing a minute spine at its centre; areolae in radial striae, striae and areolae 2.5–5 in 10 μm, smaller and closer on the elevations.

Periplekton with a circular stem 2.5–8 μm in diameter, 18–50 μm tall, straight or slightly flexuous, appressed to that of the sibling valve; ring circular or with a slight gibbosity at the top of the stem, 10–22 μm in diameter, clasping the stem of the sibling periplekton closely to moderately loosely, the two arms equal and overlapping by less than ¼ of the circumference of the ring; line joining the centres of the stems of sibling periplekta on the apical axis to perpendicular to it. Ocelli 5–7 μm in diameter, transverse and inclined at 10°–30° to the vertical. Marginal spines flat, narrowly triangular, c. 12 μm tall, absent only at the elevations, usually 2–3 in 10 μm, occasionally much sparser and 10 μm apart on one side only of the valve. No superficial spines. Mature cingulum consisting of two copulae; valvocopula closed, of uniform depth throughout, the pars exterior 18–25 μm deep with areolae much smaller than those on the valve, scattered or in vertical striae, striae 10–14 in 10 μm, areolae somewhat more widely spaced, the pars interior hyaline, 3–4 μm deep; copula II with pars exterior c. 2 μm deep.

subsp. grevilleana
Figs 1, 2, 4, 5, Plate I(a)–(c).

Valves with two elevations, symmetrical about the transapical axis.

Early Eocene. 'Kamichev', (presumed to be Kamyshlov, Sverdlovsk oblast) Russia (BM coll. Adams TS744; MANCH coll. Chaffers Kam.200).

Middle Eocene. Kuznetsk, Penza oblast, Russia (BM 36339, 74127, 74149, coll. Adams GC3008 (holotype of *Syndetoneis russica*); PH Gen. Coll. 35918).

? Indian Ocean, 4° 11.58′S, 73° 23.65′E, 2909.5 m depth, Ocean Drilling Programme, Hole 713A, core 9R–1, 102–103 cm. (Fenner & Mikkelsen, 1990, as *Rutilaria* sp.).

Cambridge, Barbados (BM 2751, 2761, 2775, 2791, 2795, 2797, 2800, 2842, 2863, 2865, 2871, 2899, 2902, 2981, 3036, 3050, 3061, 3111, 3121, 3125, 3167, 3203, 3204, 3213, 3250, 3252, 3254, 3267, 3268, 3281, 3432, 3434, 3443, 3446, 3511, 14213, 36069 (lectotype), 50082, 50083, 66804).

Middle to late Eocene. Mascarene Ridge, Indian Ocean, 10° 25′S, 63° 15′E, 3115 m depth, dredge sample. Dodo-123-D1 (BM 78176, 78177, 78178, 78179, 78180, 78202, SEM CB11.396–399, CB11.879, CB19.898, 2420, 2421; CAS 2011, 14059, 14060, 15031, 142047).

Middle Eocene–late Oligocene. Barbados (BM 64642, 75012; MANCH coll. Chaffers s.n.; PH coll. Boyer N–6–11).

Chimborazo, Barbados (BM 78210; CAS 36079).

Mount Hillaby, Barbados (BRM H8/6).

Late Eocene. Liptsy, Kharkov oblast, Ukraine. (Ol'shtynskaya, 1978).

Kantemirovka, Voronezh oblast, Russia (Strel'nikova, 1987 and personal communication).

Springfield, Barbados (BM 39450, coll. Adams G517).

Late Eocene to early Oligocene. Joe's River, Barbados (BM 36199, 65938, 76878, 78209, coll. Adams H790, SEM CB11.730, 72207–72211, 85038–85045; CAS 29072, 29073, 36078, 40082, 42080, 42081, 43021).

Forrester's Hill, Oamaru, Otago, New Zealand (BM 36099, 82236; CAS 134084).

subsp. monocellata R. Ross, subsp. nov.
Figs 3, 6, 7.

Elevatio unica in utraque valva; valvae parum transapicaliter asymmetricae.

Typus. In BRM Zu2/78, specimen no. 12, ex strato eocaenico de profundis maris Atlantici septentrionalis.

Only one elevation on each valve; valves slightly asymmetrical about the transapical axis.

Early Eocene. Blake Plateau, North Atlantic Ocean, 30° 08.54′N, 76° 06.74′W, 2665 m depth. Deep Sea Drilling Project Hole 390A, core 7, section 4, 129–131 cm (BRM Zu2/78 (holotype)).

Eocene? Gonaïves, Haiti. (G coll. Brun 4492).

The first published description of *Rutilaria grevilleana* was provided by Greville (1866). When commenting on the structure of the periplekton in *Rutilaria*, he wrote of the genus *Syndetocystis*:

> In that most wonderful genus the valves are nearly circular, fringed with ciliae [sic], and furnished with two intra-marginal rounded processes, and in the centre with another solitary process, erect, cylindrical, and elongated, and terminated by a laterally projecting ring. Looking at frustules *in situ*, in the front view, it is perceived that the stalk of the process of one valve passes through the ring of the process of the opposing valve, and, as this is the mutual position, the two frustules move freely as on pistons, and can be pulled asunder until the respective rings are brought into contact, but, of course, no further. Nothing but force can separate them.

This, as far as it goes, is an accurate description, but it was not accompanied by a figure and no specific epithet was provided. The first adequate and accurate description of the species accompanied by a figure is that provided by Ol'shtynskaya (1978) in the protologue of *Rutilaria lipica*, a synonym of *R. grevilleana*.

Ralfs had found *Rutilaria grevilleana* about the end of 1862 in fossil material from Cambridge, Barbados, that he had received from C. Johnson. Shortly after finding it, he included a description of it and some sketches in a letter to Greville dated 14 January 1863. The sketches show the periplekton as a tall spine-like process that is bent at the top into a loop that wraps round the vertical part of the periplekton of the sibling valve, and this is how it is described in the letter. In his letter Ralfs mentioned the two rounded elevations and the sketches show them. In the following year Greville wrote to a correspondent in the United States, probably H.L. Smith, describing the species and including a rough sketch drawn with a pen. This sketch shows the periplekton as drawn and described by Ralfs but the valve is

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Figs 1–7 Figs 1–2: *Rutilaria grevilleana* subsp. *grevilleana*, × 1000. Fig. 1: valve view, BM 39450, Springfield, Barbados; Fig. 2: girdle view, BM 3446, Cambridge, Barbados. Fig. 3: *Rutilaria grevilleana* subsp. *monocellata*, valve view, × 1000, BRM Zu2/78, Blake Plateau, North Atlantic Ocean, holotype. Figs 4–5: *Rutilaria grevilleana* subsp. *grevilleana*, × 1000. Fig. 4: valve, BM 36099, Forrester's Hill, Oamaru, New Zealand; Fig. 5: girdle view, BM 36069, Cambridge, Barbados, lectotype. Figs 6–7: *Rutilaria grevilleana* subsp. *monocellata*, × 1000, BRM Zu2/78, Blake Plateau, North Atlantic Ocean. Fig. 6: valve view, holotype; Fig. 7: girdle view.
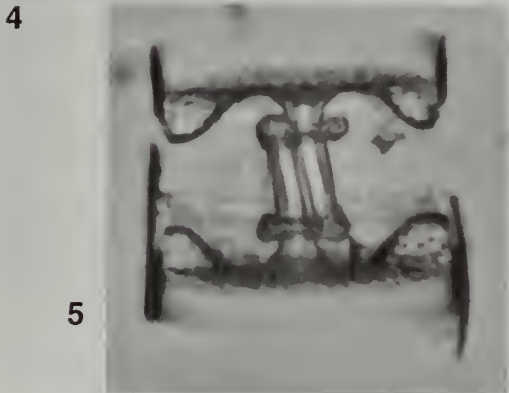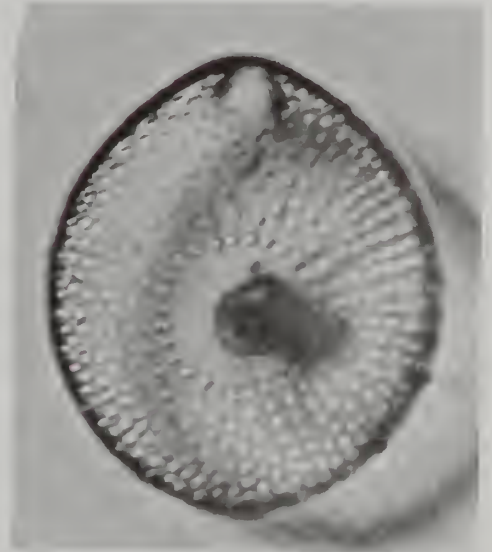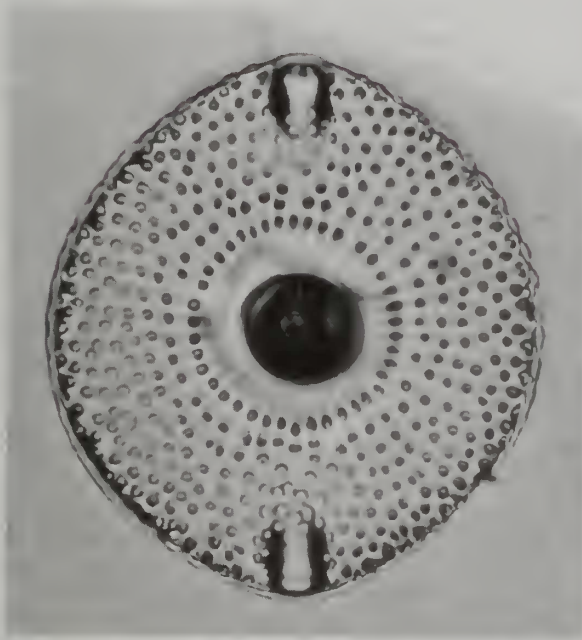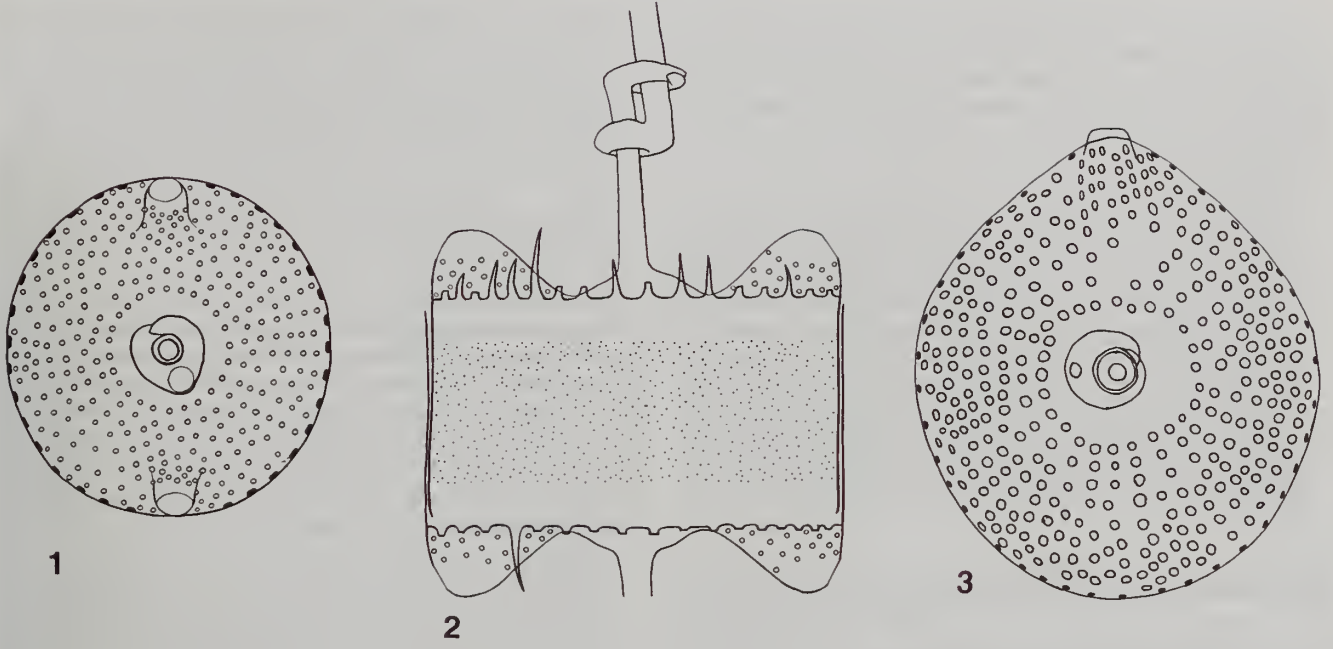
shown as a circular disc without any elevations. On the basis of this information, H.L. Smith (1872) published a short description of the genus *Syndetocystis*, and some years later Walker & Chase (1887) reproduced both the description in Greville's letter and his figure. As theirs is a rare work, the description is given here:

> *Syndetocystis Grevilleanns* [sic], (*Ralfs M.S.*) Grev. *in litt.* 1864. '– the queerest diatom I have ever had to deal with, a new genus from the Barbadoes Deposit, which Mr. Ralfs describes and which he calls *Syndetocystiss* [sic]. I have seen five frustules in a chain. The side view is a disc with radiating granules or cellules, and from the center projects a strong process which is locked into that of the adjoining disc, like a piece of machinery, so that the two frustules can be pulled asunder to the extent of the length of the processes but no further. It seems to be a special provision to prevent separation.' Cambridge Estate, Barbadoes. A faithful copy of Dr. Greville's drawing of this most strange diatom is given.

The figure given by Walker & Chase has been reproduced many times (Van Heurck, 1896, 1899; Schütt, 1896; Coupin, 1922; Karsten, 1928; Lefébure, 1947; Jurilj, 1965: fig.8). This is the earliest publication of a specific name for this species and its epithet was clearly chosen by Walker and Chase, not by Greville or Ralfs, who used the epithet *barbadensis* in the account of the species that he prepared but never published (see below).

As this is a fossil species, the original of the figure published by Walker and Chase is the holotype (Greuter et al., 1994: Art. 8.4). It is, however, impossible to say which this specimen was. It may have been one in Greville's own collection or the specimen in Ralfs's collection labelled by him '*Syndetocystis*' (BM 36069). One must accordingly choose as lectotype one of the specimens on which Greville based the description included in the protologue, and BM 36069, the one to which the generic name was first given, seems the most appropriate. I therefore designate it as lectotype.

Greville had clearly made a more careful study of *Rutilaria grevilleana* before writing the remarks on *Syndetocystis* that he published in 1866. He had also drawn some accurate figures. His correspondence with Ralfs shows that these were intended for use in the supplement to, or further edition of, Pritchard's *History of the Infusoria*, and they are not among those preserved in BM. They are described in the text accompanying A. Schmidt's (1892: Taf. 173 fig. 16) figure of the species. This figure, based on a specimen in Deby's collection (BM 14213), depicts the periplekton accurately but shows seven rounded humps around the margin. Whilst it is possible to see, when viewing the original of Schmidt's figure, how he came to misinterpret this specimen, careful examination shows that it has only two rounded elevations, each bearing an ocellus. Schmidt's legend to the figure reads:

> Barbadoes, Cambr. Est. (Deby), war als Syndetoneis? bezeichnet; aber dieser Genusname ist nach Grove von Grunow für Hemiaulus amplectens [sic] Gr. & St. vorgeschlagen. Nach drei mir von Weissflog mitgetheilten Copien von Grevilles Originalzeichnungen zu urtheilen, wäre Syndetocystis eine richtige Biddulphie mit aus der Mitte der Schalen sich erhebenden Stacheln, die sich beiderseits mit einem endständigen Ringe umklammern und sich demnach an einander verschieben können. Diese Zeichnungen sollen jedoch nicht Syndetocystis Grevilleanus Ralfs (Grevilleana!) darstellen. Weiter theilt mir

Weissflog einer Beschreibung von Syndetocystis Barbadensis Ralfs (auch von Cambr. Dep.) aus einem Manuscripte des Autors mit, welche nach seiner Ansicht auf jene Zeichnung Grevilles passt, die ich aber nicht ganz verstehe. Die hier vorliegende Zeichnung sieht nicht wie eine Biddulphiacee aus. Die Schalen werden vollständig kreisrund sein; innerhalb des mit Stacheln besetzten Randes bemerkt man c. 7 rundliche Buckeln, deren keine jedoch als ein Process gedeutet werden kann. Ein interessantes Problem für weitere Forschung.

Schmidt's figure has been reproduced by Jurilj (1965: fig. 5).

The manuscript of Ralfs's intended supplement to, or further edition of, his account of the Diatomaceae in the fourth edition of Pritchard's *History of the Infusoria* (Pritchard, 1861) came into Van Heurck's hands. He published the account of *Syndetocystis* that is included in this (Van Heurck, 1896, 1899), accompanying it, however, by a copy of the figure originally published by Walker & Chase (1887). The account, as quoted by Van Heurck, reads:

> *Syndetocystis N.G. Ralfs*. Frustules as in *Biddulphia*, but connected in a chain-like manner by strong spines from the centre of their valves. The frustules in the front view resemble those of the other genera of this family, except in having from the centre of each valve a stout central spine, which is suddenly bent near the end and curved in a link-like manner round a similar spine from the adjacent frustule. In the fossil state at least these spines slide upon each other, altering the distance between the frustules, as is well shown in fig 155˙, taken from a very perfect specimen belonging to our friend Mr Norman, of Hull.
>
> *S. Barbadensis Ralfs.*, also from Cambridge Deposit, Barbados. Mr. Johnston [sic].
>
> Valves broadly elliptical or suborbicular, with a process near each apex and one or more subulate spines, which are best seen in the front view. Surrounding the stout central spine is a large smooth portion, bordered by a circlet of pearly granules, from which radiate rows of granules.

In most works published since this, the species has been called *Syndetocystis barbadensis* but, as the figure that is part of its protologue is the same as that in the protologue of *S. grevilleanus*, the two names have the same holotype and *S. barbadensis* is an illegitimate superfluous name for *S. grevilleanus*, which provides the epithet which must be used for the species.

Pantocsek (1892) published a figure of a specimen of *Rutilaria grevilleana* from Kuznetsk, Russia, calling it *Syndetoneis russica*. This figure is an accurate representation of the periplekta of two sibling valves, but the greater part of both valves is broken away. There is no specimen labelled *Syndetoneis russica* in Pantocsek's collection in Budapest, but a specimen from Kuznetsk, mounted by Tempère, which came to BM in the collection of the late Mr F.W.Adams (BM coll. Adams GC3008) exactly matches Pantocsek's (1892) figure of *Syndetoneis russica*. It is certainly the holotype of that name. It was presumably lent to Pantocsek by Tempère, who subsequently sold it to Adams.

Another specimen of *Rutilaria grevilleana* mounted by Tempère came into the possession of Lefébure. This specimen, which came from Barbados, is mounted in valve view and consists of a single valve with an intact periplekton. It

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* As this is the number of the figure in Van Heurck's *Treatise*, it is not part of a direct quotation from Ralfs; also the figure is a copy of the one published by Walker & Chase (1887), not one that Ralfs had.

was figured by Laporte & Lefébure (1930) but they did not give it a name. They did not recognize the nature of the structure in the centre of the valve, which is not shown clearly in their illustration. Neither did Lefébure & Chenevière (1939), who based their new species, *Coscinodiscus cladiscophorus*, on this specimen and used the same figure to illustrate it.

When Ol'shtynskaya (1978) found specimens of *Rutilaria grevilleana* in the upper Eocene of the Ukraine, she did not realize that any previously published name applied to it. This is scarcely surprising in view of the inaccuracy or inadequacy of the descriptions and figures that accompanied those that did. She accordingly treated her specimens as a new species, *R. lipica*, and gave the first accurate and adequate description and figure. She remarked on the similarity of *R. lipica* to *R. limoniformis* R. Ross, although this is not very close. In consequence Strel'nikova (1987) misapplied that name, misspelling its epithet 'lymoniformis', to *R. grevilleana* when discussing the diatom stratigraphy of the Voronezh anticline. This is confirmed by a photomicrograph kindly sent me by Dr Strel'nikova.

In *Rutilaria grevilleana* the ring of the periplekton is able to slide up and down on the stem of the sibling periplekton (see Plate I (b), (c)). The only other species in which this is possible is *R. amplectans* (Grove & Sturt) R. Ross. Although some other species of *Rutilaria* have periplekta as tall as those of *R. grevilleana*, in all of these the tips of the arms of the ring are bent down towards the valve from which they arise in such a way as to prevent the sibling valves moving relative to each other (see, e.g., Plate XII (b)). *R. amplectans* differs from *R. grevilleana* in having taller periplekta and elevations, irregularly distributed and smaller areolae, and no marginal spines. There are also differences in the girdle, that of *R. grevilleana* being unique within the genus in having a closed valvocopula of uniform depth throughout.

Fenner & Mikkelsen (1990) record the occurrence of a single specimen of *Rutilaria* in middle Eocene material recovered from Ocean Drilling Project Hole 713A in the western Indian Ocean. This specimen, according to these authors, belongs to an undescribed species, and it is said to be more or less circular and with coarse radial areolation. However, these characters are those of *R. grevilleana*, which certainly occurred in the same area and at about the same geological age. It is thus highly likely that this specimen is *R. grevilleana* and that Fenner and Mikkelsen failed to recognize it because the accounts of this species in the literature, apart from Ol'shtynskaya's (1978), are so inadequate.

There are eight specimens of *Rutilaria grevilleana* on the microscope slide BRM Zu2/78 of material from the lower Eocene of the Blake Plateau, North Atlantic, and all of them have only one elevation on each valve (see Figs 3, 6, 7). They differ in no other respect from the other members of the species, but, as this feature is constant in this population and has not been found in any in which there are specimens with two elevations, it must be regarded as a distinct taxon. A single specimen showing the same feature is present on a slide in Brun's collection (at G) labelled 'Gonaïve', a town on the west coast of Haiti, normally spelled Gonaïves, that is situated about 175 km north-east of Jérémie. Brun obviously had some fossil material from there, but unfortunately nothing certain is known about its age. As their first appearances are both in the early Eocene, there is nothing to indicate the direction of the evolutionary relationship between the two subspecies.

Whilst the only firmly dated record of *Rutilaria grevilleana* subsp. *monocellata* is from the early Eocene of the Blake Plateau in the North Atlantic, *R. grevilleana* subsp. *grevilleana* has a wide distribution in both space and time. It occurs in the lower Eocene of the west Siberian plain, in the middle Eocene of the central Volga basin, in the upper Eocene of the Ukraine and of the Voronezh anticline, in the Caribbean from the middle Eocene at least up to the Eocene to Oligocene boundary, in the tropical Indian Ocean at the middle to upper Eocene boundary, and in New Zealand from very close to the boundary between the Eocene and the Oligocene. It is of interest that the only specimens found in the Oamaru diatomite come from one of the stratigraphically highest exposures of that formation. That it is known from there but not from the exposures of the formation lower in the upper Eocene is surprising; whilst this may be the result of a change in the ecological conditions, it may be no more than a consequence of haphazard preservation of a species rare in the area

2. **Rutilaria amplectans** (Grove & Sturt) R.Ross, **comb.nov.**
Figs 8–10, Plate I (d)–(f).

Hemiaulus amplectans Grove & Sturt in *J. Quekett microsc. Club*, ser. 2, **3**: 76, pl. 6 fig.17 (1887). – A. Schmidt, *Atlas Diatom.-Kunde*: Taf. 143 figs 1–3 (1889).

Biddulphia dissipata Grove & Sturt in *J. Quekett microsc. Club*, ser. 2, **3**: 134, pl. 10, fig. 16 (1887). – Grunow in *Bot. Zbl.* **34**: 37 (1888).

Hemiaulus amplectans var. *major* Grove & Sturt in *J. Quekett microsc. Club*, ser. 2, **3**: 144, pl. 13 fig. 44 (1887).

Syndetoneis amplectans (Grove & Sturt) Grunow in *Bot. Zbl.* **34**: 36 (1888). – De Toni, *Syll. alg.* **2**: 1019 (1894). – Van Heurck, *Treat. Diatom., transl. Baxter*: 425, fig. 142 (1896); *Traité Diatom.*: 425, fig. 142 (1899). – Schütt in Engler & Prantl, *Nat. Pfanzenfam.* **1**(1b): 150, fig. 280 (1896). – Karsten in Engler & Prantl, *Nat. Pfanzenfam.* 2 Aufl. **2**: 301, fig. 420 (1928). – Laporte & Lefébure, *Diatom. rares cur.* **2**: pl. 16 fig. 111 (1930). – L.D.Coombs in *Microscope* **8**: 300, figs 1–3 (1952); in *Microscope* **9**: 24 (1952). – Jurilj in *Acta bot. croat.* **24**: 74, figs 1–4 (1965). – Tsumura in *J. technol. Res., Yokohama* **12**: 238, pl. 2 fig. 10 (1967). – Desikachary & Sreelatha, *Oamaru Diatoms. Biblioth. Diatomol.* **19**: 242, pl. 109 figs 3–7 (1989). – Reed in Edwards in *Palaeont. Bull. Wellington* **64**: 144, pl. 8 figs 101, 102 (1991).

Odontella dissipata (Grove & Sturt) De Toni, *Syll. alg.* **2**: 866 (1894).

Syndetoneis amplectans var. *major* (Grove & Sturt) F.W. Mills, *Index Diatom.*: 1547 (1935). – Desikachary & Sreelatha, *Oamaru Diatoms. Biblioth. Diatomol.* **19**: 243, pl. 109 figs 2, 8 (1989).

Frustules with the pervalvar axis equalling the apical axis to up to four times its length. Valves depressed at the centre, with cylindrical apical elevations rounded at their summits, 20–26(–45) μm tall, 5–7 μm in diameter; valves 20–100 μm long, 15–70 μm wide, elliptical, rounded to obtuse at the apices. A hyaline marginal ridge 2.5–3 μm tall extending from elevation to elevation. Mantle vertical, 7–8 μm deep, hyaline. Central area circular, its diameter ¼ of the breadth of the valve in the largest specimens to rather more than ½ in the smallest. Areolae small, *c.* 0.5 μm in diameter, occluded externally by domed vela with minute spines around their

margins; areolae irregularly scattered, 2–4 in 10 μm. Periplekton with a circular stem 3–5 μm in diameter, 50–65(–115) μm tall, straight or very slightly flexuous, appressed to that of the sibling valve; ring circular, *c.* 12.5 μm in diameter, clasping the stem of the sibling periplekton closely to moderately loosely, the arms equal and overlapping by about ⅓ of the circumference of the ring; line joining the centres of the stems of sibling periplekta on the apical axis to perpendicular to it. Ocelli 3–5 μm in diameter, transverse or slightly inclined to the transapical axis, inclined at *c.* 45° to the vertical, porelli *c.* 50 in 10 μm. No marginal spines. Small curved superficial spines 1–2 μm tall and 2–5 μm apart, a few of them bifurcate, on the proximal side of the elevations. Mature cingulum consisting of three copulae; valvocopula with its abvalvar margin very deeply indented at one pole, 30–45 μm deep; copula II with a strongly developed ligula and a smaller anti-ligula opposite; copula III with its advalvar margin indented opposite the anti-ligula of copula II; each copula with a single or double row of areolae *c.* 20 in 10 μm close to its advalvar margin, elsewhere areolae in interrupted vertical striae, striae and areolae *c.* 20 in 10 μm where gaps not present, but randomly distributed gaps much more frequent than areolae.

Middle to late Eocene. Mascarene Ridge, Indian Ocean, 10° 25′S, 63° 15′E, 3115 m depth, dredge sample, Dodo – 123–D1 (CAS 2036).

[**Middle Eocene–late Oligocene.** Barbados (BM 63391).]

Late Eocene. Oamaru, Otago, New Zealand (BM 11146, 11152, 11153, 14302 (=Tempère & Peragallo, Diatomées no. 50) Jackson's Paddock, 14454 (=Tempère & Peragallo, Diatomées no. 200) Totara, 32717 Jackson's Paddock, 33206, 33211, 33313 Jackson's Paddock, 33316 Jackson's Paddock, 33317 Jackson's Paddock, 33318 Jackson's Paddock, 33319 Jackson's Paddock, 35403 Dick's Farm, 35919 Lower Papakaiyo, 36305, 41402, 46592 (holotype of *Hemiaulus amplectans*), 46601, 46608 (holotype of *Hemiaulus amplectans* var. *major*), 46609, 46631 (holotype of *Biddulphia dissipata*), 46632, 52698, 52740 Jackson's Paddock, 53064 Jackson's Paddock, 56529 Jackson's Paddock, 60658, 60659 Jackson's Paddock, 63389, 63390, 64642, 64687, 66183, 68486 (=Tempère & Peragallo, Diatom. Monde ent. no. 140) Bain's Farm, 71082 Jackson's Paddock, 74131 Jackson's Paddock, 74132, 74133, 74147, 76863, 77754 Jackson's Paddock, 77756 Totara, 77758 Allan's Farm, 77759, 77760, 90987 Jackson's Paddock, 91015, 91017, 91031, coll. Adams Bess.978, C675, C677, G59, G85 Railway Cutting, G103 Cormack's Siding, G111, G126 Totara, G162 Jackson's Paddock, G163 Jackson's Paddock, G168 Jackson's Paddock, G589 Cormack's Siding, G623, G668, GC3007, GC3305 Troublesome Gulley, J325, J326, TS23, TS271, TS272 Jackson's Paddock, TS292, coll. Guthrie 499, coll. Morley Jones s.n. Allan's Farm, s.n. Allan's Farm & Dick's Farm, SEM B1.194, B2.364–365 Dick's Farm, B2.369 Dick's Farm, EM1.366–366a, CB10.94–103, CB16.793–808, CB16.847, 9742, 72172–72177, 72671–72678; BRM H.t.98, H.t.99, H.t.100; CAS 134083, 134085, 139080 Jackson's Paddock, 139081); G coll. Brun 2566, 152D Bain's Farm, lower; MANCH coll. Chaffers C15, C16, K1, K4, o355, o356, coll. Slatter 4 no. 2 Jackson's Paddock, s.n.; PH Gen. Coll. 89074, 89242 Borrie's, coll. Boyer L–4–22 Allan's Farm; US 7285 Totara, 7286 Jackson's Farm, 7287 Jackson's Farm, 7288 Cormack's Siding, 7289 Totara).

? **Eocene**. Gonaïves, Haiti. (G coll. Brun 4492).

It would seem that Sturt drew the figures that illustrate the new species described in Grove and Sturt's account of the diatoms in the deposit at Oamaru, New Zealand. No specimens in either Grove's or Sturt's collections, both now in BM, are labelled as being the originals of their figures. They can often be recognized as such, however, by the fact that they match the illustrations precisely. This is so for *Hemiaulus amplectans*, *H. amplectans* var. *major* and *Biddulphia dissipata* and their holotypes are in BM 46592 (Fig. 10), BM 46608 and BM 46631 respectively.

The epithet adopted for this species by Grove and Sturt, *amplectans*, means 'winding or twining round'. It is the present participle of the deponent verb *amplector*, which was normally treated by classical Latin authors as belonging to the third declension, its present participle being spelled '*amplectens*'. This caused A. Schmidt (1889) to treat the original spelling as an orthographic error; he writes 'amplectens Gr. & St., nicht amplectans!'. In this he was followed by De Toni (1894), Van Heurck (1896, 1899), Schütt (1896), Karsten (1928) and Jurilj (1965). However, there is one place in the writings of Plautus where the verb is treated as belonging to the first declension. Plautus is an early author who is considered by classical scholars to have written less good Latin than such later authors as Livy and Cicero. Nevertheless, this example shows that *amplector* could be treated as belonging to the first declension, and it is thus not obvious that the original spelling is an orthographic error; it should therefore not be altered.

Rutilaria amplectans differs from all the other species of the genus by having tall cylindrical elevations (see Fig 10, Plate I (d)). The presence of these caused Grove & Sturt (1887a), when they first described it, to place it in the genus *Hemiaulus* Heiberg, nom. cons., although they suggested that it would perhaps be better placed in a genus of its own. Grunow (1888), in his comment on Grove and Sturt's account of this species, recognized that this was so and proposed for it the new generic name *Syndetoneis*. It is not completely clear, however, whether he gave that generic name, and the combination *S. amplectans*, valid publication or whether these names were first validly published by De Toni (1894) a few years later (see p. 11 above).

Rutilaria amplectans has taller periplekta than any other species of the genus, and the stems of these are often slightly flexuous (Fig 10, Plate I (d)). In consequence, the ring of the periplekton is frequently to the side of stem, i.e. the line joining the centre of the ring and the centre of the stem is parallel to the transapical axis rather than the apical axis. This is the case on one of the two valves of the holotype specimen (Fig. 10). As its two periplekta are thus at right angles to one another, Grove & Sturt's (1887a) correctly drawn illustration shows them as different, one as an obvious ring projecting to one side from the top of the stem, the other as projecting equally on either side of the stem. This caused some authors, e.g. De Toni (1894), Van Heurck (1896, 1899), to assume that the two periplekta of a pair of sibling valves differed, and that this distinguished *Syndetoneis* from *Syndetocystis* at the generic level. Grunow (1888), on the other hand, considered that the two genera had similar periplekta but differed by the absence of elevations in *Syndetocystis*.

Because of the length of the periplekta and the way in which they hold pairs of sibling valves together, most specimens of this species consist of two sibling valves lying in girdle
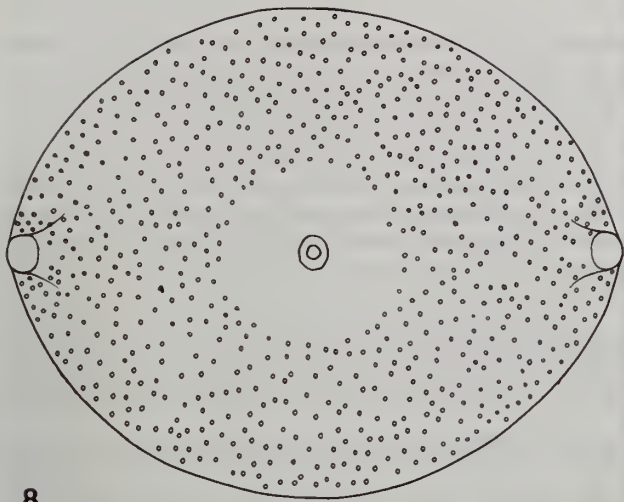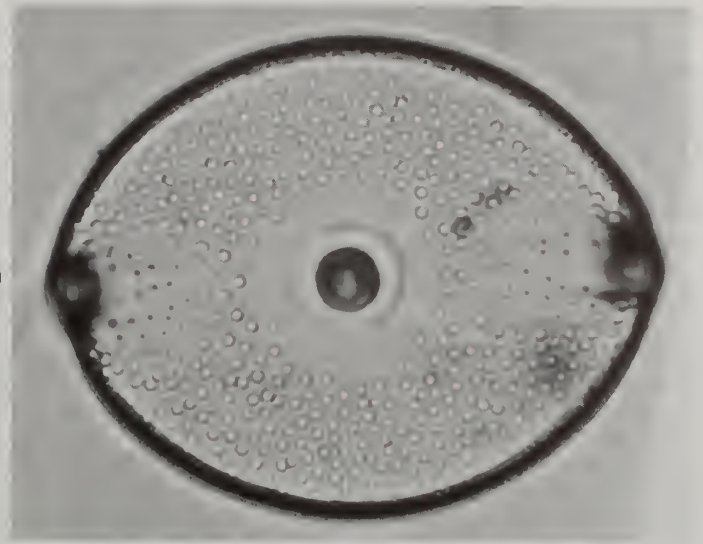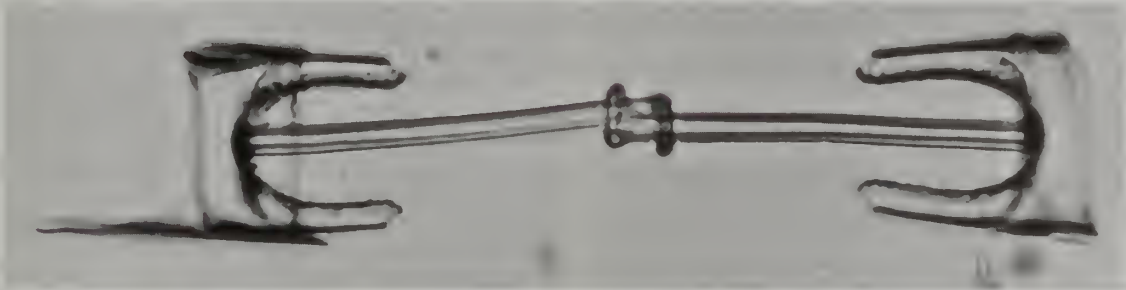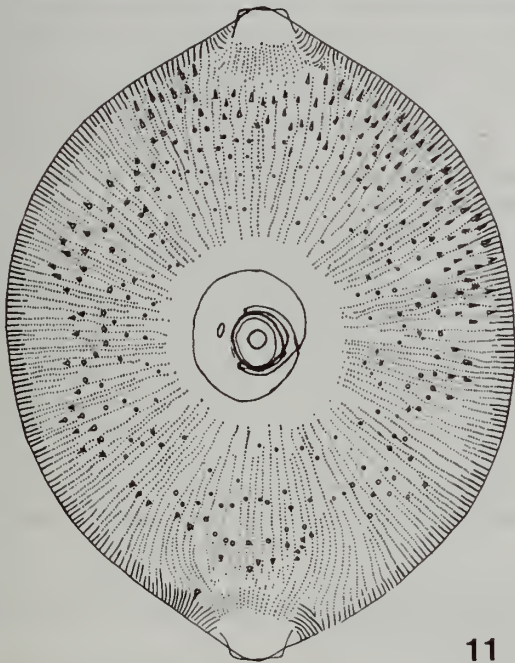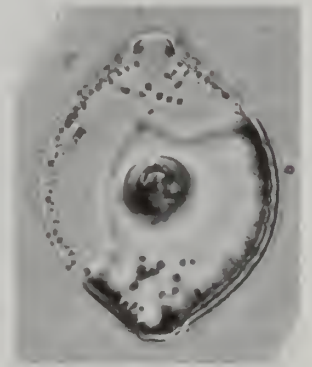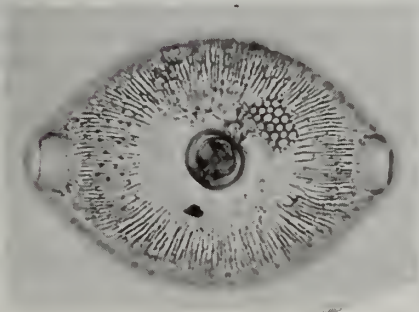
Figs 8–14 Figs 8-10: *Rutilaria amplectans*, × 1000. Figs 8–9: valve view, × 1000, BM 35919, Lower Papakaiyo, Oamaru, New Zealand; Fig. 10: girdle view, BM 46592, Oamaru, New Zealand, holotype. Figs 11–12: *Rutilaria erinaceus*. Fig.11: valve view, × 1000, CAS 216041, Falkland Plateau, South-western Atlantic Ocean, holotype; Fig. 12: valve view, × 500, Ninety East Ridge, Indian Ocean. (photograph A. Gombos). Figs 13–14: *Rutilaria limoniformis*, × 1000, Falkland Plateau, South-western Atlantic Ocean. Fig. 13: valve view, CAS 216021, holotype; Fig. 14: valve view, BM 78200.

view, and such specimens are readily recognizable. However, when Grove & Sturt (1887*b*) encountered a specimen that was a single valve lying in valve view and with the periplekton broken off, they did not realize what it was but described it as a new species of *Biddulphia* S.F.Gray, *B. dissipata*. This was treated as an independent species until its true identity was pointed out by Coombs (1952).

Grove & Sturt (1887*b*) also described *Hemiaulus amplectans* var. *major*, distinguishing it from the type of the species on the basis of larger valves that were punctate, not hyaline. There is, however, a continuous range of size in the specimens of the species from Oamaru and the type of this varietal name (in BM 46608) does not fall outside it. Also, all the specimens of the species, including its type (in BM 46592), have areolate valves. There are no grounds, therefore, for recognizing varieties within the species, as most authors have realized. The one specimen I have seen from the Indian Ocean has, however, much taller elevations and periplekta than any specimens from Oamaru, although its apical axis is short, 28 μm; the elevations are 45 μm tall and the periplekta 115 μm tall, the maximum heights for Oamaru specimens being 26 μm and 65 μm respectively.

Rutilaria amplectans is not infrequent in the upper Eocene deposit at Oamaru, New Zealand. It is not, however, common. Doig (in Edwards, 1991) records only two specimens, one from Allan's Farm (AF1) and one from Jackson's Paddock (JP3), in lists of the diatom assemblages in 42 samples from 12 sections, each list based on 300–500 specimens. It is apparently rarer in the slightly earlier dredge sample from the Indian Ocean, from which I have seen one specimen only. I have also seen one specimen from the deposit of uncertain but probably Eocene age from Gonaïves, Haiti, that Brun studied; its frequency there is uncertain as no more than a number of selected specimens from this material have been available for examination. The only other *Rutilaria* from this locality is *R. grevilleana* subsp. *monocellata* R. Ross, known otherwise only from the lower Eocene of the Blake Plateau in the North Atlantic Ocean. If the Gonaïves deposit was contemporary with this, the record of *R. amplectans* from there is the earliest occurrence of the species.

There is also a specimen of *R. amplectans* (BM 63391) sold by Messrs Watson & Sons, Ltd.; its label, reading 'Syndetoneis amplectans. Barbados', was written by one of their staff. No other specimen from Barbados has been found in spite of the intensive study of the fossil diatoms from that island. Other specimens sold by Watson's have manifest clerical errors on their labels (see p. 24 sub *R. radiata*) and the possibility that this is so in this case also cannot be discounted. Although the species is present at another locality in the Caribbean, this specimen cannot be regarded as providing a certain record of its occurrence in Barbados.

3. **Rutilaria erinaceus** R. Ross in *Occ. Pap. Calif. Acad. Sci.*
   123: 21, pl. 1 fig. 1 (1976).
   Figs 11, 12.

Valves slightly depressed in the centre and sloping upwards at each apex to form slight elevations; valves 89–100 μm long, 67–70 μm wide, broadly ovate, with very slightly produced obtuse apices. Central area circular or very slightly elliptical, *c*. 24 μm in diameter. Areolae in often slightly sinuous radial striae of varying lengths, striae *c*. 11 in 10 μm except near the margin, where they are closer and *c*. 14 in 10 μm, areolae *c*. 22 in 10 μm. Periplekton with a circular stem *c*. 6 μm in

diameter, *c*. 25 μm tall, appressed to that of the sibling valve; ring slightly elliptical, 14–15 μm by 16–18 μm, the arms equal, overlapping by *c*. ⅓ of the circumference of the ring, and with their tips bent towards the valve from which they arise; line joining the centres of the stems of sibling periplekta strongly inclined to the apical axis of the valves. Ocelli 6–10 μm in diameter, transverse, inclined at 10°–20° to the vertical. No marginal spines. Superficial spines 2–5 μm apart throughout the valve face except on or close to the central area.

Paleocene. Ninety East Ridge, Indian Ocean, 11° 20.21′S, 88° 43.08′E, 1670 m depth. Deep Sea Drilling Project Hole 214, core 38-2, 100–102 cm (Gombos, personal communication).

Paleocene–middle Eocene. Falkland Plateau, south-western Atlantic Ocean, 47° 28′ 7″S, 59° 20′ 6″W, 1167 m depth. Vema cruise 12, core 46, 630 cm. (CAS 216041 (holotype*)).

The holotype of *Rutilaria erinaceus* (Fig. 11 and Ross, 1976: fig. 1) is the only specimen of the species that I have seen. This has no element of the girdle attached. The photomicrograph of another specimen kindly sent me by Dr Gombos (Fig. 12) also shows a valve without any girdle attached.

Rutilaria erinaceus is very similar to *R. limoniformis* R. Ross, which is known from the middle and upper Eocene. The characters by which the two species differ are discussed below under *R. limoniformis*. There are also considerable similarities between *R. erinaceus* and *R. grevilleana* (Walker & Chase) R. Ross both in outline and in the dimensions of the periplekton, but *R. grevilleana* has much more prominent elevations than *R. erinaceus*, its areolae are much larger and more widely spaced, and it has marginal spines but no superficial spines. Also, the tips of the arms of the periplekton of *R. erinaceus* are bent down towards the valve from which they arise, preventing the sibling valves from sliding towards and away from one another in the way which is possible in *R. grevilleana*.

This species is very rare in the sample from the Falkland Plateau from which the holotype comes. No other specimen has been found in this material, which is mainly middle Eocene in date, but with a strong admixture of Paleocene and early Eocene forms (Fenner in litt., 1984). The specimen of which Dr Gombos sent me a photomicrograph comes from the upper Paleocene recovered from DSDP Site 214 in the Indian Ocean. This suggests that the holotype is also of Paleocene date.

The epithet of this species, *erinaceus*, a hedgehog, is a noun in apposition, not an adjective. It refers to the sharp spines that are distributed over most of the valve.

4. **Rutilaria limoniformis** R. Ross in *Occ. Pap. Calif. Acad. Sci.* **123**: 23, pl. 1 fig. 4 (1976).
   Figs 13, 14.

Valves slightly depressed in the centre and sloping upwards at each apex to form slight elevations; valves 40–48 μm long, 32–33 μm broad, broadly ovate with slightly produced obtuse apices. Central area circular, 14–17 μm in diameter. Areolae scattered or in much interrupted radial striae that converge towards the apices, striae *c*. 20 in 10 μm, areolae *c*. 25 in 10 μm, but very rarely in continuous rows of more than eight, the longest rows of areolae being in those striae that are

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* The diatom collection at CAS has been re-numbered since 1976, hence the different number for this holotype from that in Ross, 1976.

directed towards the apices. Periplekton with a circular stem *c.* 3 μm in diameter, *c.* 18 μm tall, appressed to that of the sibling valve; ring slightly longer than wide, 8.5–10 μm × 7–8.5 μm, closely clasping the stem of the periplekton of the sibling valve, the arms equal and overlapping by *c.* ¼ of the circumference of the ring, their tips much narrowed beyond the point where they meet and bent towards the valve from which they arise; line joining the centres of the stems of sibling periplekta inclined to the apical axes of the valves. Ocelli *c.* 3 μm in diameter, transverse and vertical. Marginal spines pointed, in a single, sometimes rather irregular, row reaching to the apices, 6–8 in 10 μm. Superficial spines sparsely scattered between the central area and the apices, pointed.

Middle Eocene. Falkland Plateau, south-western Atlantic Ocean, 51° 08′S, 54° 22′W, 1525 m depth. Vema cruise 17, core 107, 50 cm (BM 78200), 120 cm (CAS 216021 (holotype*)).

Neither of the specimens of *Rutilaria limoniformis* that have yet been found has any element of the girdle attached.

Rutilaria limoniformis resembles *R. erinaceus* R. Ross in many ways; the valves are similar in outline and in the shape and proportions of the elevations and ocelli, the periplekta of both are comparatively tall, are set obliquely on the valves and have rings with equal arms. *R. limoniformis* differs, however, from *R. erinaceus* by its much smaller size, its much interrupted striae and its definite row of marginal spines. Whilst it seems probable that there is a close phylogenetic relationship between *R. limoniformis* and the older *R. erinaceus*, it is unlikely that the former is a direct descendant of the latter; the absence of marginal spines in *R. erinaceus* seems to be a derived character.

Rutilaria limoniformis is rare in the middle Eocene material from the Falkland Plateau and it is not known from any other locality. Strel'nikova (1987), who mis-spelled the epithet '*lymoniformis*', recorded it as characterizing an upper Eocene zone in the deposits of the Voronezh anticline, but a photograph of a specimen from this material kindly sent me by Dr Strel'nikova shows that this record is based on misidentified specimens of *Rutilaria grevilleana* (Walker & Chase) R. Ross. When Ol'shtnyskaya (1978) described *R. lipica*, a synonym of *R. grevilleana*, as a new species, she said that it resembled *R. limoniformis*, and this apparently caused Strel'nikova to consider the two synonymous.

5. **Rutilaria interrupta** R. Ross in *Occ. Pap. Calif. Acad. Sci.* **123**: 22, pl. 1 figs 2, 3 (1976).
Figs 15, 16, Plate II (a)–(d).

Valves depressed in the centre, with sub-circular flat-topped apical elevations *c.* 2 μm tall, *c.* 5 μm in diameter; valves 55–230 μm long, 20–30 μm wide, with a central portion with parallel or slightly concave margins, tapering gradually into shorter or longer projections 7–12 μm wide with rounded-cuneate, sometimes slightly subcapitate, apices. A hyaline marginal ridge 1–2 μm tall extending from elevation to elevation. Mantle vertical, 4–6 μm deep, hyaline. Central area extending to the margins. Areolae *c.* 0.2 μm in diameter, in radial striae 20–25 in 10 μm close to the central area but much more distant and interrupted towards the apices,

areolae 18–25 in 10 μm; areolae not reaching the margin of the valve face but leaving a hyaline border *c.* 2 μm wide. Periplekton with a circular stem *c.* 6 μm in diameter, 10 μm tall, straight or slightly curved, 3–4 μm distant from that of the sibling valve; ring subtriangular to circular with a prominent bulge at the top of the stem, 20–27 μm × 17.5–22 μm, clasping the stem of the sibling periplekton closely to moderately loosely, the arms equal and with a long overlap, their tips bent towards the valve from which they arise and meeting; line joining the centres of the stems of sibling periplekta on, or slightly inclined to, the apical axis. Ocelli large, transverse, vertical or slightly inclined, curved around the apex of the valve. No marginal or superficial spines.

Middle Eocene. Falkland Plateau, south-western Atlantic Ocean, 51° 08′ S, 54° 22′ W, 1525 m depth. Vema cruise 17, core 107, 50 cm (BM 82238, 82241; CAS 216042 (holotype*)), 120 cm (BM 78450, CAS 82034, 83032, 216029), 175 cm (CAS 216024), 245 cm (BM SEM 35947–35956), level in core not noted (BM 78197, SEM CB.14.149–153).

Middle to late Eocene. South-western Atlantic, 53° 01′ S, 52° 42′ W, 2880 m depth. Vema cruise 18, core 104, 330–335 cm (CAS 216023).

Middle–late Eocene. South-western Atlantic, 47° 45.7′ S, 57° 38.5′ W, 3650 m depth. Conrad cruise 12, core 237 (BM 78201).

No specimen of *Rutilaria interrupta* with any element of the girdle attached has been seen.

Rutilaria interrupta is one of a group of elongate species with large periplekta with equal arms, and close areolae in radial rows, *R. radiata* Grove & Sturt, *R. hannai* R. Ross and *R. kamyshlovensis* R. Ross being the others. In *R. radiata* there is a range of length from individuals with no projections to others with projections that are much longer than the central portion of the valve and are subcapitate (see Fig. 19). Whether as wide a range is present in the other species is uncertain because of the small number of specimens available. However, those of *R. interrupta* that have been seen range from ones with very short projections to others in which these are long and subcapitate, suggesting that it too might have a range as wide as that in *R. radiata*. The most obvious character that distinguishes *R. interrupta* from the other members of this group is the size of its periplekton relative to the width of the valve, together with the fact that the large hyaline central area reaches the margins of the valve; in the other species the central area is completely surrounded by striae, although those of *R. hannai* subsp. *diomedeae* R. Ross are mostly of only one areola. These other species also differ in having marginal spines and no more than a slight marginal ridge, whereas *R. interrupta* has a prominent marginal ridge but no marginal spines.

The ring of the periplekton varies in shape between subtriangular (Fig. 16) and circular with a bulge at the head of the stem (Plate II (d)), and the closeness with which the arms of the ring clasp the stem of the periplekton of the sibling valve also varies somewhat. When this species was originally described, it seemed possible that these differences might be correlated with the geological age of the specimens, but since then further specimens from the middle Eocene have been seen and these show that this variation occurred within the population of that age.

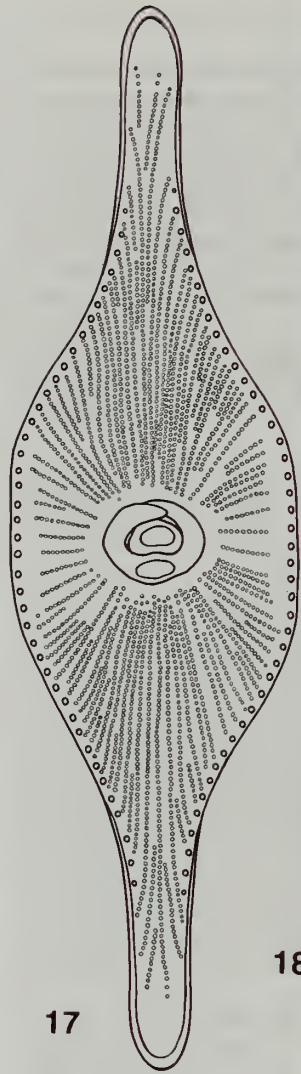So far, at least, *Rutilaria interrupta* is known only from the

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* The diatom collection at CAS has been re-numbered since 1976, hence the different number for this holotype from that in Ross, 1976.
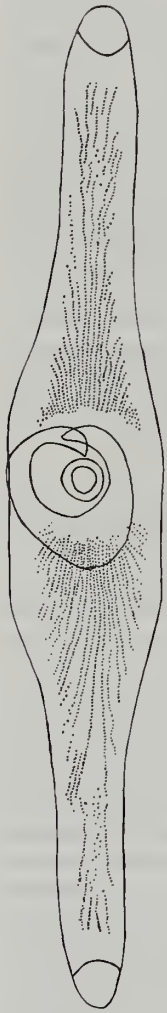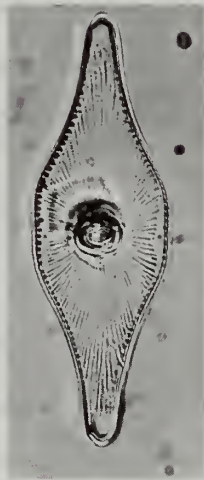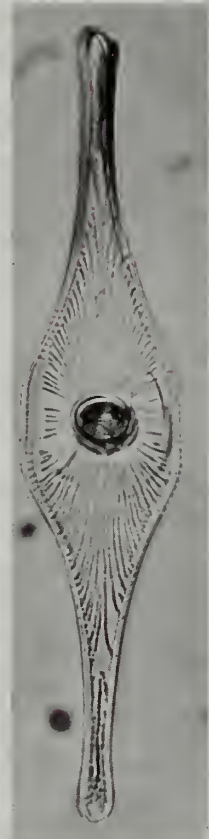
15

16

17

18

19

a

b

c

d

e

middle to late Eocene of the south-western Atlantic. It thus appears later in the fossil record than *R. kamyshlovensis* but earlier than the other two species to which it is closely related.

6. **Rutilaria radiata** Grove & Sturt in *J. Quekett microsc. Club*, new ser. **2**: 323, pl. 18 figs 4, 5 (1886). – Lautour in *Trans. Proc. N. Z. Inst.* **21**: pl.22 fig. 10 (1889). – A. Schmidt, *Atlas Diatom.-Kunde*: Taf. 183 figs 21–23 (1893). – De Toni, *Syll. alg.* **2**: 1022 (1894). – Laporte & Lefébure, *Diatom. rares cur.* **1**: pl. 3 fig. 19 (1929). – Tsumura in *Bull. Yokohama City Univ. Soc.* **16**, Nat. Sci. 1: 90, pl. 3 figs 1, 2 (1964). – Jurilj in *Acta bot. croat.* **24**: 77, figs 9, 10 (1965). – Desikachary & Sreelatha, *Oamaru Diatoms. Biblioth. Diatomol.* **19**: 226, pl. 97 figs 1–10 (1989). Figs 17–19, Plate III (a)–(d).

Rutilaria superba sensu J.D.Möller, *Diatom.-Präp.*: Taf. 6 Reihe 6 no. 6–8, Taf. 26 Reihe 5 no. 12–13 (1891); *Verz. Lichtdrucktaf. Möll. Diat.-Präp.*: 44, 164 (1892), non Greville.
Rutilaria excavata Brun in *Diatomiste* **2**: 87, pl. 5 figs 18, 19 (1894).
Rutilaria epsilon sensu Reed in Edwards in *Palaeont. Bull. Wellington* **64**: 144, pl. 8 figs 97, 98 (1991).

Frustules up to 50 μm deep but usually less. Valves depressed in the centre and with very slight or no apical elevations; valves 55–240 μm long, 25–50 μm wide, with parallel margins to the central portion, and tapering cuneately to narrowly rounded apices or to obtuse or subcapitate projections with rounded apices, the projections *c.* 5 μm wide, sometimes expanding to *c.* 7 μm wide at their apices. A very slight marginal ridge extending from elevation to elevation. Mantle vertical, 7–8 μm deep, hyaline. Central area circular, 16–18 μm in diameter. Areolae *c.* 0.3 μm in diameter, occluded by domed vela, in distant radial striae of varying length, striae 5–10 in 10 μm, areolae 15–17 in 10 μm; areolae not reaching the margin of the valve face except along the projections but leaving a hyaline margin *c.* 4 μm wide opposite the central area and narrowing towards the projections or, where these are absent, the apices. Periplekton with an elliptical stem, its major axis transverse and *c.* 7 μm, *c.* 20 μm tall, sinuous, appressed to that of the sibling valve; ring with a transversely elliptical outline, 10.5–11.5 μm × 11.5–14.5 μm, the arms equal and with a long overlap, their tips bent towards the valve from which they arise and meeting those of the sibling valve; line joining the centres of the stems of sibling periplekta on the apical axis or inclined at no more than 5° to it. Ocelli *c.* 5 μm in diameter, transverse, vertical, porelli 50–70 in 10 μm. Marginal spines pointed, 10–12 μm tall, almost reaching the apices on specimens without or with only short projections but absent on the distal parts on those with longer projections, 5–6 in 10 μm. No superficial spines. Mature cingulum consisting of at least four copulae; valvocopula 10–12 μm deep but only *c.* 6 μm deep at one apex; copula II 10–12 μm deep: copula III 4–9 μm deep; copula IV 3–6 μm deep; copulae II–IV with a ligula at one apex of the frustule,

ligulae of adjacent bands at opposite apices; copulae with areolae in vertical striae, striae 20–24 in 10 μm, areolae 15–20 in 10 μm.

[**Early Eocene**. Sengilei, Ulyanovsk oblast, Russia (BRM H.t.44).]

Late Eocene. Oamaru, Otago, New Zealand (BM 7383, 8725, 9280, 11095, 11096, 11141, 11148, 11152, 11250 Jackson's Paddock, 11252, 14302 (= Tempère & Peragallo, Diatomées no. 50) Jackson's Paddock, 14454 (= Tempère & Peragallo, Diatomées no. 200) Totara, 14455 (= Tempère & Peragallo, Diatomées no.201) Totara, 14456 (= Tempère & Peragallo, Diatomées no. 202) Bain's Farm, lower, 14457(= Tempère & Peragallo, Diatomées no. 203) Bain's Farm, lower, 14479 (= Tempère & Peragallo, Diatomées no. 225) Troublesome Gully, 14480 (= Tempère & Peragallo, Diatomées no. 226) Troublesome Gully, 14482 (= Tempère & Peragallo, Diatomées no. 228) Jackson's Well, 14523 (= Tempère & Peragallo, Diatomées no. 269), 30818 Jackson's Paddock, 31328, 32715, 32717 Jackson's Paddock, 33207, 33208, 33211, 33313 Jackson's Paddock, 33317 Jackson's Paddock, 33318 Jackson's Paddock, 33319 Jackson's Paddock, 34284 Williams' Bluff, 35032 Dick's Farm, 35394 Dick's Farm, 35919 Lower Papakaiyo, 36124 Dick's Farm, 36304 Allan's Farm, 41673, 41674, 46542, 46544, 46547, 46567, 46568, 46571, 46574 (lectotype, see p. 24), 46579, 46583, 46592, 46601, 46631, 52698, 52703, 52709, 52718, 52735, 52737, 52745, 52748, 52754, 52761, 52767, 55784, 56819, 56820, 60838, 60839 Jackson's Well, 60841, 63396 Cave Valley, 64684, 64687, 64754, 66564, 66566, 66571, 68348 (= Tempère & Peragallo, Diatom. Monde ent., ed. 2, no. 2) Jackson's Paddock, 68486 (= Tempère & Peragallo, Diatom. Monde ent., ed. 2, no. 140) Bain's Farm, 68487 (= Tempère & Peragallo, Diatom. Monde ent., ed. 2, no. 141) Bain's Farm, 69161 (= Tempère & Peragallo, Diatom. Monde ent., ed. 2, no. 810) Troublesome Gully, 69162 (= Tempère & Peragallo, Diatom. Monde ent., ed. 2, no. 811) Troublesome Gully, 69163 (= Tempère & Peragallo, Diatom. Monde ent., ed. 2, no. 812) Troublesome Gully, 69166 (= Tempère & Peragallo, Diatom. Monde ent., no. 815) Totara, 70423, 70424, 70425, 71085, 71086, 71095, 71101, 71104, 71105, 73746, 74143, 74144 Totara, 74145, 74146, 76084, 76336, 76346, 76748, 76863, 76950 Dick's Farm, 77754 Jackson's Paddock, 77756, 77757, 77760, 77761, 91003, 91013, 91014, 91015, coll. Adams A922 Cormack's Siding, Bess.299, Bess.659 Railway Cutting, C495, C496, G6, G7, G14, G28, G30, G41, G43, G44, G47, G57, G60, G68 Railway Cutting, G103 Cormack's Siding, G106 Allan's Farm, G109, G111, G133 Troublesome Gully, G136, G156 Jackson's Paddock, G158 Jackson's Paddock, G162 Jackson's Paddock, G167 Jackson's Paddock, G168 Jackson's Paddock, G587, G605, G615 Totara, G620 Railway Cutting, G622 Totara, G626, G641 Totara, G652 Troublesome Gully, G653, G654 Allan's Farm, G657, G668, GC1036 Troublesome Gully, GC2718, GC2719, GC2720, GC2721, GC2722, GC3305 Troublesome Gully, H216, J568, J817 Jackson's Paddock, L35 Allan's Farm, TS23, TS54 Mataura, TS270, TS271, TS272 Jackson's Paddock, TS292, TS433,

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Figs 15–19   Figs 15–16: *Rutilaria interrupta*, × 1000, Falkland Plateau, South-western Atlantic Ocean. Fig. 15: valve view, CAS 216042, holotype; Fig. 16: valve view, BM 78197. Figs 17–18: *Rutilaria radiata*, × 1000, Oamaru, New Zealand. Fig. 17: valve view, BM coll. Adams G6; Fig. 18: valve view, BM 46574, lectotype. Fig. 19: *Rutilaria radiata*, specimens in valve view showing outline variation, × 500; a: BM 36124, Dick's Farm, Oamaru, New Zealand; b: BM 11095, Oamaru, New Zealand; c: BM 70423, Oamaru, New Zealand; d, e: BM coll. Morley Jones s.n., Oamaru, New Zealand.

TS949 Bain's Farm, lower, coll. Bastow 855 Jackson's Pad-
dock, coll. Guthrie 485 Papakaiyo, 499, s.n., coll. Morley
Jones s.n., s.n. Allan's Farm, s.n. Allan's Farm, s.n. Bain's
Farm, lower s.n. Dick's Farm, s.n. Papakaiyo, SEM
B1.189–193, B1.198, B1.201–202, B1.207–209, B1.348,
B1.350, B1.353–354, B1.356–366. B1.543–557, B2.371–372
Lower Papakaiyo, B11.559, 561, 563, 565 Allan's Farm,
B12.209–210 Allan's Farm, EM2.36–38, CB16.858–860,
CB17.694–703, 2747–2750, 72290–72294, 72767–72777; BRM
H.t.38 Williams' Bluff, H.t.39, H.t.40, H.t.41, H.t.42, H.t.43
Totara, H.t.53 Totara, N.16.87; CAS 126038 Flume Gully,
130024 Flume Gully, 130025 Flume Gully, 131065 Flume
Gully, 134075 Totara, 139039, 139041; G coll. Brun 204D
Totara (holotype of *Rutilaria excavata*), 1885, 2257 Bain's
Farm, lower, 2400; MANCH coll. Chaffers o357, o358, o359;
PH Gen. coll. 20090, 89073, 89165 Jackson's Paddock, coll.
Boyer B-2-6, Q-3-4 Totara, U-3-26 Jackson's Paddock; US
7212 Totara, 7213, 7214 Cormack's Siding, 7215 Cormack's
Siding, 7216 Cormack's Siding, 7217, 7218 Cormack's Siding,
7219 Cormack's Siding, 7220 Cormack's Siding, 7221 Tot-
ara).

Late Eocene to early Oligocene. Forrester's Hill, Oamaru,
New Zealand (BM 36100).

[**Miocene**. California, U.S.A. (CAS 355040).]

[**Late Miocene**. Malaga Cove, Los Angeles County, Califor-
nia, U.S.A. (PC coll. Lefébure s.n.).]

Grove & Sturt (1886) provided two figures of *Rutilaria
radiata* along with its original description, but whilst one (pl.
18 fig. 4) shows details of the structure the other (pl. 18 fig. 5)
just indicates the different outline of another specimen. The
original of the former, if it could be identified, is thus the
holotype. There are a number of specimens of this species in
BM that were in the possession of either Grove or Sturt at the
time when they were preparing their account of the diatom
flora in the fossil deposit from Oamaru, New Zealand. None
of them is annotated as being the original of either of the
figures accompanying its original description. It seems, how-
ever, that the figures provided by Grove and Sturt were
drawn by Sturt, and one of the three specimens on a slide
from his collection, BM 46574 (Fig. 18), closely matches pl.
18 fig. 4 of their paper. It is probably the holotype, but this is
not certain, and I therefore designate it here as the lectotype.
  Rutilaria radiata is one of the species in which the length of
the valve, and with it the outline, varies greatly, the shortest
valves being hexagonal and the longer ones having projec-
tions of varying length, the longest of which are subcapitate
(see Fig. 19). It is sufficiently common in the late Eocene
material from Oamaru for its range of variation to have been
obvious to Grove and Sturt when they were preparing the
original account of the diatoms in this deposit. They drew
attention to this when describing the species and provided an
outline figure of a sub-hexagonal valve (Grove & Sturt, 1886:
pl. 18 fig. 5) as well as a detailed one of a much longer
specimen with projections (pl. 18 fig. 4). In consequence, *R.
radiata* has no synonyms based on differences in outline,
unlike the other species of *Rutilaria* known to have a similar
range, *R. elliptica* Greville, *R. philippinarum* Cleve & Grove
and *R. obesa* Cleve. Except for the variation in the length and
outline of the valve, *R. radiata* is very uniform.
  It is possible that the girdle of *Rutilaria radiata* is similar to
that of *R. kamyshlovensis* R. Ross and has a valvocopula that

is narrowed at one end and open at the other. No scanning
electron micrographs that would show this are available and it
is not possible to be certain on this point from examination by
light microscopy.
  Rutilaria hannai R. Ross is the species that most closely
resembles *R. radiata*, but it differs in the outline of its central
portion and the shape of its periplekton. *R. kamyshlovensis*
has more closely spaced areolae and striae than *R. radiata*, a
periplekton of a different shape, marginal spines that inter-
lock, and large elevations at the apices. The remaining
elongate species to have periplekta with equal arms, *R.
interrupta* R. Ross, also has raised elevations at the apices
and differs from *R. radiata* in addition by being without
marginal spines and by having a central area reaching the
margin of the valve.
  Möller (1891, 1892) identified specimens of this species as
Rutilaria superba Greville, a synonym of *R. elliptica* Greville,
a very different species with a much smaller periplekton with
unequal arms and also with much more distant areolae.
  Brun (1894) described *Rutilaria excavata* as having a hya-
line valve. The only specimen with this name in his collection
is a selected one mounted in girdle view and is the original of
his fig. 19. Careful examination of this with the light micro-
scope shows that it has radiating striae and that it is a
specimen of *R. radiata* without projections. It would seem
that Brun's figure of a specimen in valve view (1894: fig. 18) is
based on observations made before it was mounted, possibly
combined with an attempt to arrive at the appearance in this
view from optical sections of the girdle view. This opinion is
strengthened by the way in which the periplekton is depicted.
If this were seen as clearly as it is indicated, something much
more nearly resembling the true structure would have been
shown.
  Rutilaria radiata occurs throughout the upper Eocene
deposit at Oamaru, New Zealand. There is a specimen in
BRM labelled as coming from 'Singiliewsky', i.e. from Seng-
ilei in the middle Volga basin, Russia. The deposit exposed
there is probably early Eocene in date, although it may be
late Paleocene. As no other specimen of the species has been
found in this material, which has received much attention
from many workers, it seems very probable that this speci-
men is a stray. This is also true of the specimen in PC labelled
as coming from Santa Monica, i.e from the upper Miocene of
Malaga Cove, California (see Hanna, 1928b, 1936), another
much studied deposit. In addition, there is a specimen of the
species in CAS on a slide sold by W. Watson and Sons and
labelled as being *Rutilaria hexagona* from California; this is
clearly a case of the wrong label being put on the slide. One
can accordingly safely say that *R. radiata* is known only from
the upper Eocene of Oamaru, New Zealand.

7. **Rutilaria hannai** R. Ross, **sp. nov.**

Frustula 25–35 μm alta, fortasse nonnumquam altiora. Val-
vae ad centrum depressae, sine elevationibus apicalibus,
portione centrali circulari vel late elliptica, in projecturas
obtusas vel subcapitatas angustata; 55–220 μm longae, 28–47
μm latae; projecturae 4–9 μm latae, eae subcapitatae ad
apices 6–13 μm latae. Axes apicales valvarum fraternarum
paralleli. Limbus ab fronte angulo separatus, *c*. 7 μm altus,
hyalinus. Area centralis circularis, magna, diametro 18–33
μm. Areolae diametro *c*. 0.2 μm, in strias radiales dispositae,
eas areae centrali oppositas ex 1–6 areolis constantes, eas in
projecturis multum interruptas; striae ad margines areae

centralis 18–25 in 10 μm, distaliter distantiores, areolae 22–30 in 10 μm; areolae ad marginem frontis non attingentes sed taenia hyalina 3–6 μm lata areae centrali opposita per projecturas decrescens. Periplekton caule circulari diametro 4–10 μm, ab eo valvae fraternae 1–4 μm distanti, annulo circulari ad summum caulis plus minusve gibboso, 14–24 μm × 13–18 μm, ex brachiis duobus aequalibus constanti; brachia longe imbricata, ubi superposita attenuata, caulem valvae fraternae perfecte cingentia et arcte amplectentia. Ocelli diametro 4–8 μm, transversi, ab verticali 10°–15° inclinati, porellis *c.* 50 in 10 μm. Spinae marginales acutae, ad centrum valvae *c.* 7 μm altae, apices versus breviores, 3–4 in 10 μm, in partibus distalibus projecturarum valvarum longiorum absentes. Spinae superficiales nullae vel paucae, in parte distali portionis centralis valvae et in parte proximali projecturarum dispersae.

Typus. CAS 104086, ex stratis eocaenicis ad 'Cantua Creek, Fresno County, California, U.S.A.'

Frustules 25–35 μm deep, possibly sometimes deeper. Valves depressed in the centre and without any elevations at the apices; valves 55–220 μm long, 28–47 μm wide, with a circular or broadly elliptical central portion tapering into obtuse or subcapitate projections, the projections 4–9 μm wide, expanding to 6–13 μm wide at their apices when these are subcapitate. Mantle separated from the valve face by a sharp angle, vertical, *c.* 7 μm deep, hyaline. Central area circular, large, 18–33 μm in diameter. Areolae *c.* 0.2 μm in diameter, in radial striae, those on the projections much interrupted, striae 18–25 in 10 μm at the margins of the central area, becoming more widely spaced distally, areolae 22–30 in 10 μm; striae opposite the central area of 1–6 areolae, areolae not reaching the margin of the valve face but leaving a hyaline area 3–6 μm wide opposite the central area that becomes narrower along the projections. Periplekton with a circular stem 4–10 μm in diameter, 1–4 μm distant from that of the sibling valve; ring circular with a slight to large bulge at the head of the stem, 14–24 μm × 13–18 μm, clasping the stem of the sibling periplekton closely, the arms equal, with attenuate tips bent towards the valve from which they arise and completely encircling the stem of the sibling periplekton; line joining the centres of the stems of sibling periplekta on the apical axis. Ocelli 4–8 μm in diameter, transverse, inclined at 10°–15° to the vertical, porelli *c.* 50 in 10 μm. Marginal spines *c.* 7 μm tall at the centre of the valve, shorter towards the apices, pointed, absent on the distal part of the projections of longer valves, 3–4 in 10 μm. Superficial spines none or few, pointed, scattered on the distal part of the central portion of the valve and on the proximal part of the projections.

subsp. **hannai**
Figs 20, 21, Plate IV (a)–(f).

Rutilaria kerneri sensu Sheshukova-Poretskaya, *Neogen. Morsk. Diatom. Vodor. Sakhalina Kamchatki*: 236, tabl. 41 fig. 4 (1967), non Pantocsek.

Portio centralis valvae late elliptica ad circularis; valvae 55–170 μm longae, 28–40 μm latae; projecturae 4–8 μm latae, eae longiores subcapitatae. Striae areae centrali oppositae ex 1–6 areolis constantes. Caulis periplekti diametro 4–6 μm, ab eo valvae fraternae 3–4 μm distans, annulo ad summum caulis parum gibboso, 15 μm × 13–14
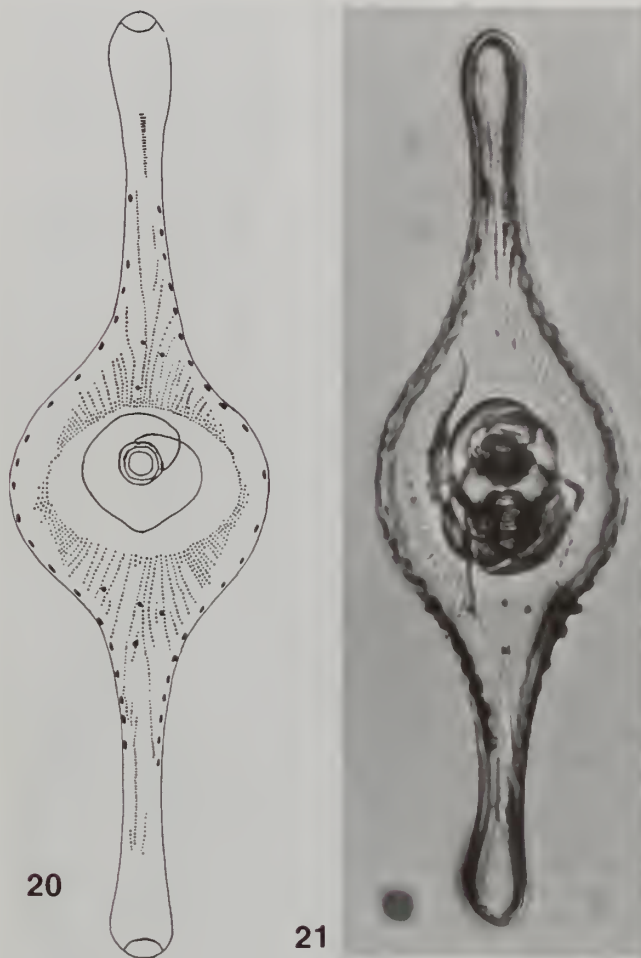
Figs 20–21 *Rutilaria hannai* subsp. *hannai*, valve view, × 1000, CAS 104086, Cantua Creek, Fresno County, California, U.S.A., holotype.

μm. Cingulum ex quatuor taeniis constans; valvocopula et copula II quaeque parte exteriori *c.* 6 μm alta; copula III parte exteriori *c.* 5 μm alta; copula IV parte exteriori *c.* 2 μm alta; valvocopula, copula II et copula III areolis in striis verticalibus 27–28 in 10 μm, copula IV areolis in striis verticalibus 34–36 in 10 μm.

Central portion of the valve broadly elliptical to circular; valves 55–170 μm long, 28–40 μm wide; projections 4–8 μm broad, the longer ones subcapitate. Striae opposite the central area consisting of 1–6 areolae. Stem of periplekton 4–6 μm in diameter, 3–4 μm distant from that of the sibling valve, ring with a slight bulge at the head of the stem, 15 μm × 13–14 μm. Cingulum consisting of four copulae; valvocopula and copula II with the pars exterior *c.* 6 μm deep; copula III with the pars exterior *c.* 5 μm deep; copula IV with the pars exterior *c.* 2 μm deep; valvocopula, copula II and copula III with areolae in vertical striae 27–28 in 10 μm; copula IV with areolae in vertical striae 34–36 in 10 μm.

Late Eocene. Bassendorf Shale, south end of Coos Bay, Coos County, Oregon, U.S.A., California Academy of Sciences sample no 1612, leg. H.G. Schenk (BM 82237, CAS 216045).
 Kreyenhagen Shale, mined earth by Panoche Road,

Panoche Hills, Fresno County, California, U.S.A. (CAS 110017).

200–300 feet (60–90 m) below top of Lillis Shale, Cantua Creek, Fresno County, California, U.S.A. (BM SEM 97986–97990, 97995–97996, 98048–98049, 112974, 112976, 112979; CAS 104086 (holotype)).

Late Eocene to early Oligocene. Anadyr River, Magadanskaya Oblast, eastern Siberia, Russia (Sheshukova-Poretskaya, 1967).

subsp. **diomedeae** R. Ross, **subsp. nov.**
Figs 22, 23.

Portio centralis valvae circularis; valvae 190–220 μm longae, 41–47 μm latae; projecturae 7–9 μm latae, apicibus 11–13 μm latis. Striae areae centrali oppositae pro parte maxima ex areola una constantes. Caulis periplekti diametro 7–10 μm, ab eo valvae fraternae *c.* 1 μm distans, annulo ad summum caulis fortiter gibboso, 22–24 μm × 17.5–18 μm.

Typus. In BM coll. Adams TS 481, ex stratis miocaenicis de profundis maris Pacifici borealis.

Central portion of the valve circular; valves 190–220 μm long, 41–47 μm wide; projections 7–9 μm broad, expanding to 11–13 μm broad at their apices. Striae opposite the central area mostly of one areola only. Stem of periplekton 7–10 μm in diameter, *c.* 1 μm distant from that of the sibling valve, ring with a large bulge at the head of the stem, 22–24 μm × 17.5–18 μm.

Early Miocene. Aleutian Basin, Bering Sea, 54° 47′ 20″ N, 179° 08′ 00″ W, 1670 m depth. U.S.S. Albatross Station 4029H (BM coll. Adams TS481 (holotype), TS547).

Rutilaria hannai is a rare species. Subsp. *hannai* is known from only four localities, in each of which it is infrequent or rare, and subsp. *diomedeae* is also rare in the one locality from which it is known. Only a small number of specimens of subsp. *hannai* have been seen and of these only one, examined with the scanning electron microscope, is a frustule in girdle view (Plate IV (b) and (d)). The descriptions of the frustule as a whole and of the cingulum are based on this one specimen and in consequence do not indicate the range of variation that almost certainly exists. The two specimens of subsp. *diomedeae* both consist of a pair of sibling valves mounted in valve view; there is accordingly no information about its girdle. Also, it is impossible to know the full range of variation in length of either subspecies and whether this includes specimens without any projections; too few specimens are available. However, the ten specimens of subsp. *hannai* that have been seen have a range in length wide enough to suggest that this subspecies at least may be as variable as *R. radiata* and include specimens without projections, but whether this is so also in subsp. *diomedeae* is much more uncertain.

Rutilaria radiata Grove & Sturt is the species that resembles *R. hannai* most closely. The characters that distinguish them from one another, and from *R. interrupta* R. Ross and *R. kamyshlovensis* R. Ross, the other similar species, are discussed above under *R. radiata* (p. 24).

There is too little morphological difference between the two subspecies of *Rutilaria hannai* for them to be treated as separate species, even although the ages of the fossil deposits in which they occur are separated by an appreciable gap.

Subsp. *hannai* is the older, occurring in late Eocene deposits in California and Oregon, and it is also present in the late Eocene to Oligocene from the left bank of the lower Anadyr River, eastern Siberia. The specimen from there described and figured by Sheshukova-Poretskaya (1967) under the name *Rutilaria kerneri* Pantocsek is clearly misidentified. The size and shape of its periplekton and the arrangement of its areolae make it plain that it is not *R. obesa* Greville ex Cleve, of which *R. kerneri* is a synonym. Although the specimen is somewhat shorter than the few from the western U.S.A. (it is only 55 μm long; they range from 85 μm to 170 μm in length), the figure shows that it has the shape, the size of the central area, and the distribution of the areolae that are characteristic of *R. hannai* subsp. *hannai*, and that the size of the periplekton is as found in that species. According to the description, the striae are 16–22 in 10 μm and both superficial and marginal spines, not shown in the figure, are present. The record from the Anadyr River can therefore be referred to *R. hannai* subsp. *hannai* with confidence, especially as it is from a deposit of similar age to those in the western U.S.A. where the subspecies is found.

The only material in which specimens of *Rutilaria hannai* subsp. *diomedeae* have been found is the sample dredged by U.S.S. Albatross at Station 4029H in the southern Bering Sea. This is of early Miocene age (see p. 6 above), and subsp. *diomedeae* is thus younger than subsp. *hannai* and also than the species most closely related to it, *Rutilaria kamyshlovensis* R. Ross, *R. interrupta* R. Ross, and *R. radiata* Grove & Sturt. There is no selected specimen of this subspecies in US; one cannot therefore tell whether Mann saw any example of it when preparing his account of the diatoms collected by U.S.S. Albatross (Mann, 1907). If he did, he presumably included it within his extraordinarily wide concept of *Rutilaria epsilon* (see p. 57 below).

It seems appropriate to name *Rutilaria hannai* after Dr G.D. Hanna, who contributed so much to our knowledge of fossil diatoms, especially those of the western U.S.A., and who selected and mounted specimens of the species from Oregon. The sample from which subsp. *diomedeae* came was collected by U.S.S. Albatross, and the subspecific epithet is derived from the generic name of the bird after which that ship was named.

8. **Rutilaria kamyshlovensis** R. Ross, **sp. nov.**
Figs 24–26, Plate V (a)–(f).

*Rutilaria longicornis* sensu Jousé in *Notul. syst. Inst. cryptog. Horti bot. petropol.* **10**: 101, fig. 2 (1955), non Brun & Tempère.
Rutilaria sp. Krotov & Shibkova in *Notul. syst. Inst. cryptog. Horti bot. petropol.* **12**: 128, fig. 5(13) (1959).

Valvae ad centrum non depressae, elevationibus apicalibus supra planis *c.* 10 μm longis et *c.* 5 μm altis, portione centrali elongata, elliptica, projecturis aliquantum latis, nonnumquam subcapitatis, apicibus rotundatis, 95–310 μm longae, 25–50 μm latae, projecturae 6–10.5 μm latae, eae subcapitatae ad apices 10–18 μm latae. Axes apicales valvarum fraternarum paralleli. Limbus ab fronte angulo separatus, *c.* 4 μm altus, hyalinus. Area centralis elliptica, latitudine *c.* dimidium valvae. Areolae diametro *c.* 0.3 μm, in parte centrali valvae in strias radiales dispositae, striae *c.* 15 in 10 μm, areolae 20–24 in 10 μm, in projecturis irregulariter dispositae et aliquantum distantiores, in summis elevationum in strias
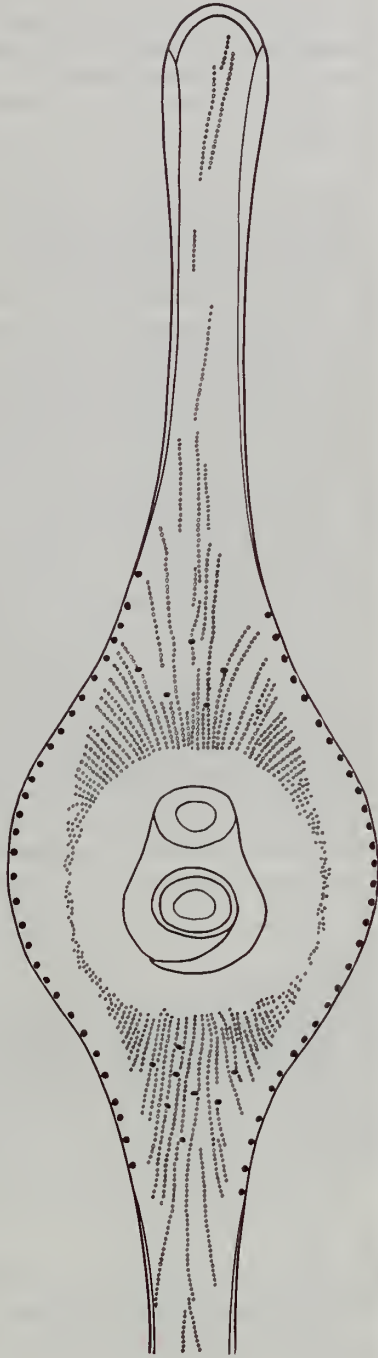
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23

Figs 22–23 *Rutilaria hannai* subsp. *diomedeae*, valve view, × 1000, BM coll. Adams TS481, Aleutian Basin, Bering Sea, holotype.

longitudinales c. 18 in 10 μm dispositae; areolae ad marginem frontis non attingentes sed taenia hyalina c. 2 μm lata secus marginem. Periplekton caule circulari diametro 2.5–3 μm, 10–12 μm alto, recto, ad eum valvae fraternae appresso, annulo subquadrato diametro c. 12 μm periplekton valvae fraternae arcte amplectenti, ex brachiis duobus aequalibus constanti; brachia longe imbricata, ubi superposita angustatissima, ad fines paene approximata. Ocelli diametro c. 8 μm, transversi, fere verticales, porellis 40–45 in 10 μm. Spinae marginales crassae, ad apices fere attingentes, c. 12 μm altae, in portione centrali valvae 2.5–4 in 10 μm, super expansae atque intricatae et ad basim tuberculo minimo instructae, in projecturis distantiores et acutae. Spinae superficiales nullae. Cingulum ex quatuor minimum taeniis constans; valvocopula parte interiori hyalina c. 2.5 μm alta et parte exteriori c. 7 μm alta sed apicem clausum versus decrescens et 4 μm alta; copula II parte exteriori c. 5 μm alta; copula III parte exteriori c. 4 μm alta; copula IV parte exteriori c. 2 μm alta; copulae II–IV quaeque ligula bene evoluta instructa; partes exteriores copularum omnium striis verticalibus 25–30 in 10 μm ex areolis 18–25 in 10 μm constantibus instructae.

TYPUS. BM 78360 ex stratis eocaenicis ad 'Kamichev', Rossiam.

Valves not depressed at the centre, with flat-topped apical elevations c. 5 μm tall, c. 10 μm long; valves 95–310 μm long, 25–50 μm wide, with an elongate elliptical central portion, and relatively broad and sometimes subcapitate projections rounded at the apices, the projections 6–10.5 μm wide, expanding to 10–18 μm wide at their tips when these are subcapitate. Mantle separated from the valve face by a sharp angle, vertical, c. 4 μm deep, hyaline. Central area elliptical, its breadth about half that of the valve. Areolae c. 0.3 μm in diameter, in radial striae in the central part of the valve, striae c. 15 in 10 μm, areolae 20–24 in 10 μm, irregularly arranged and somewhat more distant on the projections, in longitudinal striae c. 18 in 10 μm on the tops of the elevations; areolae not reaching the edge of the valve face but leaving a hyaline border c. 2 μm wide. Periplekton with a circular stem 2.5–3 μm in diameter, 10–12 μm tall, straight, appressed to that of the sibling valve; ring with a subquadrate outline c. 12 μm in diameter, clasping the periplekton of the sibling valve closely, the arms equal and with a long overlap, the overlapping portions much narrowed, their tips bent towards the valve from which they arise and almost meeting; line joining the centres of the stems of sibling periplekta slightly inclined to the apical axis. Ocelli c. 8 μm in diameter, transverse, almost vertical, the porelli 40–45 in 10 μm. Marginal spines stout, c. 12 μm tall, extending almost to the apices, on the central portion of the valve expanded at their tips and interlocking, with a very small tubercle on the outer side at the base, 2.5–4 in 10 μm, on the projections pointed and somewhat more distant. No superficial spines. Mature cingulum consisting of at least four copulae; valvocopula an open band, the pars interior hyaline, c. 2.5 μm deep, the pars exterior c. 7 μm deep but narrowed to c. 4 μm deep at the closed apex; copula II with pars exterior c. 5 μm deep and a well developed ligule; copula III with pars exterior c. 4 μm deep; copula IV with pars exterior c. 2 μm deep; all copulae with vertical striae, striae 25–30 in 10 μm, areolae 18–25 in 10 μm.
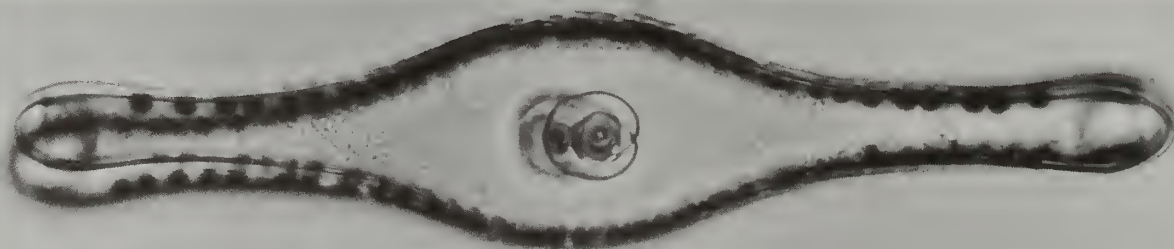
Early Eocene. 'Kamichev' (presumed to be Kamyshlov, Sver-
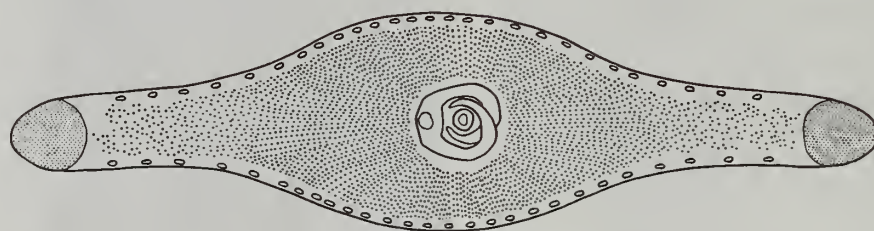
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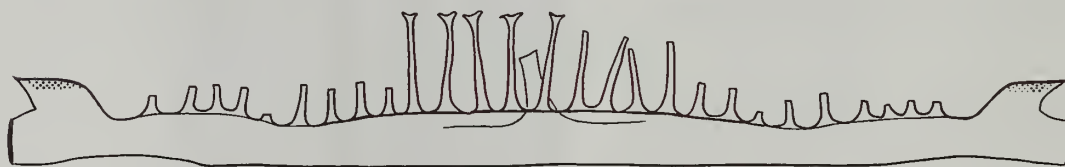
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Figs 24–26 *Rutilaria kamyshlovensis*, × 1000, 'Kamichev', Russia. Fig. 24: valve view, specimen lost; Fig. 25: girdle view, BM 36245; Fig. 26: valve view, BM 78360, holotype.

dlovsk oblast, Russia) (BM 36244, 36245, 78360 (holotype), coll. Morley Jones s.n., SEM CB18.718–719, CB18.730–735, 59928–59933, 59935, 72201, 72202, 112962–112966, 112968, 112969; BRM Zt.1.41; CAS 52029; MANCH coll. Chaffers Kam46; Jousé, 1955*).

Irbit, Sverdlovsk oblast, Russia (Krotov & Shibkova, 1959).

No complete frustule of *Rutilaria kamyshlovensis* has been seen, although a specimen examined with the scanning electron microscope consists of two attached sibling valves, one of them with a complete girdle but not the other valve of the frustule, attached.

Rutilaria kamyshlovensis resembles *R. interrupta* R. Ross, *R. radiata* Grove & Sturt and *R. hannai* R. Ross in having large periplekta with equal arms, valves with projections, and close areolae in more widely spaced radial striae. It differs from these three species, however, by having marginal spines that are expanded above and interlocking and have tubercles at their bases (Plate V (c)). Interlocking marginal spines with tubercles at their bases are otherwise only found in species with small periplekta with unequal arms. *R. kamyshlovensis* also differs from *R. radiata* and *R. hannai* by having raised elevations at the apices. *R. interrupta*, which has raised elevations, has no marginal spines.

Jousé (1955) identified a specimen of *Rutilaria kamyshlovensis* from Kamyshlov as *Rutilaria longicornis* Brun & Tempère, a synonym of *R. epsilon* Greville, but her figure clearly shows the characteristics of *R. kamyshlovensis*. *R. epsilon* has very unequal arms to its periplekta, its areolae are irregularly scattered and it has superficial spines. None of these characters are present in *R. kamyshlovensis*. Krotov & Shibkova (1959) were uncertain whether the incomplete specimen that they found and figured belonged to the same species as Jousé's, but their figure makes it plain that it did. Glezer & Sheshukova-Poretskaya (1968) record *R. epsilon* var. *longicornis* from the upper Eocene from near Dnepropetrovsk in the Ukraine. They are likely to have based their identification on Jousé's account of *R. longicornis*, but their figures (tabl. II figs 8*a*, *b*) show that the taxon that they found there is *R. tenuicornis* subsp. *paleogena* R. Ross.

Rutilaria kamyshlovensis is known only from the lower Eocene deposit at Kamyshlov on the eastern slopes of the central Ural mountains, and from the nearby deposit at Irbit, probably of the same age.

9. **Rutilaria minima** Hustedt ex R. Ross, **sp. nov.**

? *Rutilaria longirostris* Anisomova in Proshkina-Lavrenko et al., *Diatom. Analiz* 2: 216 (1949), nom. invalid., fossilis sine figura.

Frustula 6–7 μm alta. Pars marginalis frontis marginem versus decliva, frons ad centrum leviter depressa; valvae elevationibus apicalibus abrupte elevatis *c*. 1.5 μm altis et 1.25–2 μm longis, anguste rhombicae aut portione centrali elliptica vel anguste elliptica in projecturas angustas, interdum curtissimas, gradatim decrescenti, 12–60 μm longae, 5–11 μm latae, projecturis, quum adsunt, 1.25–2 μm latis. Limbus 0.5–1 μm altus, hyalinus, ab fronte costa marginali *c*. 0.25 μm alta separatus. Area centralis circularis, diametro 3–7.5 μm. Areolae diametro 0.2–0.7 μm, vel prope marginem frontis in striis ex 2–4 areolis constantibus, alibi

irregulariter, vel ubique irregulariter, dispositae. Periplekton caule circulari diametro 0.75–1.5 μm, 3.5–5 μm alto, ad eum valvae fraternae approximato, annulo diametro 3–6 μm, ex brachiis inaequalibus constanti; brachia margine alata *c*. 1 μm lata in parte proximali, finibus attenuatis, eo longiori *c*. 300°, eo curtiori *c*. 120° extenso. Ocelli diametro *c*. 1 μm, transversi, ab verticale *c*. 45° inclinati. Spinae marginales superficialesque nullae sed costa *c*. 1 μm alta ab margine utraque frontis 1–2 μm distans, area centrali opposita irregularis vel interrupta, in parte distali valvae singula et centraliter posita. Cingulum ex copulis duabus apertis constans; valvocopula parte interiori *c*. 0.5 μm alta et parte exteriori *c*. 2 μm alta, serie una advalvari areolarum 15–35 in 10 μm, saepe irregulariter dispositarum, ornata; copula II parte exteriori *c*. 1 μm alta, serie una advalvari areolarum *c*. 40 in 10 μm ornata.

TYPUS. In BM 36335 ex stratis palaeocaenicis ad Inza, Ulyanovsk oblast, Russia.

Frustules 6–7 μm deep. Valve face with the marginal part sloping downwards, slightly depressed at the centre; valves with abruptly raised apical elevations *c*. 1.5 μm tall and 1.25–2 μm long, narrowly rhombic or with an elliptical or narrowly elliptical central portion tapering into narrow, sometimes very short, projections, 12–60 μm long, 5–11 μm wide, the projections, when present, 1.25–2 μm wide. Mantle 0.5–1 μm deep, hyaline, separated from the valve face by a marginal ridge *c*. 0.25 μm tall. Central area circular, 3–7.5 μm in diameter. Areolae 0.2–0.7 μm in diameter, in short striae of 2–4 areolae close to the margin and irregularly arranged elsewhere, or irregularly arranged throughout. Periplekton with a circular stem 0.75–1.5 μm in diameter, 3.5–5 μm tall, close to that of the sibling valve, ring 3–6 μm in diameter, the arms unequal, with a flange *c*. 1 μm broad on their proximal part and with narrowed tips, the longer extending for *c*. 300°, the shorter for *c*. 120°; line joining the centres of the stems of sibling periplekta at *c*. 30° to the apical axis. Ocelli *c*. 1 μm in diameter, transverse, inclined at *c*. 45° to the vertical. No marginal or superficial spines but a costa *c*. 1 μm tall inset 1–2 μm from either margin of the valve face, irregular or interrupted opposite the central area, single and central on the distal part of the valve. Cingulum consisting of two open copulae; valvocopula with a pars interior *c*. 0.5 μm deep and a pars exterior *c*. 2 μm deep, with a single advalvar row of areolae 15–35 in 10 μm, often irregular; copula II with a pars exterior *c*. 1 μm deep and a single advalvar row of areolae *c*. 40 in μm.

subsp. **minima**
Figs 27, 28, Plate VI (a)–(d).

Valvae portione centrali elliptica vel anguste elliptica, in projecturas angustas, interdum curtissimas, gradatim decrescenti, 12–45 μm longae, 7–11 μm latae. Areolae diametro *c*. 0.2 μm, prope marginem frontis in striis curtis 16–20 in 10 μm ex 2–4 areolis constantibus, alibi irregulariter et 12–15 in 10 μm dispositae.

Valves with an elliptical or narrowly elliptical central portion tapering into narrow, sometimes very short, projections, 12–45 μm long, 7–11 μm wide. Areolae *c*. 0.2 μm in diameter, in short striae of 2–4 areolae and 16–20 in 10 μm near the margin of the valve, elsewhere irregularly arranged and 12–15 in 10 μm.

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* This record is from Kamyshlov, not 'Kamichev'.

Paleocene. Inza, Ulyanovsk oblast, Russia (BM 36335 (holo-type), 36336, SEM 113320–113325).

   ? Ulyanovsk oblast, Russia (Proshkina-Lavrenko et al., 1949).

   ? Penza oblast, Russia (Proshkina-Lavrenko et al., 1949).

subsp. **danica** R. Ross, **subsp. nov.**
Figs 29, 30.

Rutilaria sp. Homann in *Geol. Jb.*, A, **123**: 104, Taf. 34 figs 13–18 (1991).

Valvae anguste rhombicae, 28–60 μm longae, 5–8 μm latae. Areolae prope aream centralem diametro *c.* 0.25 μm, alibi majores et diametro 0.5–0.7 μm, ubique irregulariter disposi-tae.

TYPUS. In BM 82225 ex stratis paleocaenicis vel eocaenicis inferioribus ad 'Knudeklint' in insula 'Für', Dania.

Valves narrowly rhombic, 28–60 μm long, 5–8 μm broad. Areolae *c.* 0–25 μm in diameter near the central area, larger and 0.5–0.7 μm in diameter elsewhere, irregularly arranged throughout.

Paleocene to early Eocene. Silstrup, Thy, Denmark (Homann, 1991).

   Hanklit, Mors, Denmark (Homann, 1991)

   Knudeklint, Fur, Denmark (BM 82225 (holotype), 82228; Homann, 1991).

   Skarrehage, Denmark (Homann, 1991)

The late Dr F. Hustedt, when examining the fine fraction of fossil material from Inza, detected small specimens of *Ruti-laria* which were, he thought, all of one species. He gave them the manuscript name *R. minima*. He kindly presented two strewn slides of this material to BM so that they would be available to me during the preparation of this monograph. Close examination, however, showed that four different species, *R. minima*, *R. hustedtii* R. Ross, *R. delicatula* R. Ross and *R. hyalina* R. Ross, were present on these slides, but the one which he had marked by a ring on the cover-glass is this species. These species are very similar in size and outline, but *R. minima* is readily distinguished from the others by the fact that it has no marginal or superficial spines but instead has a continuous costa in the position where marginal spines occur in other species (Plate VI (a), (d)).
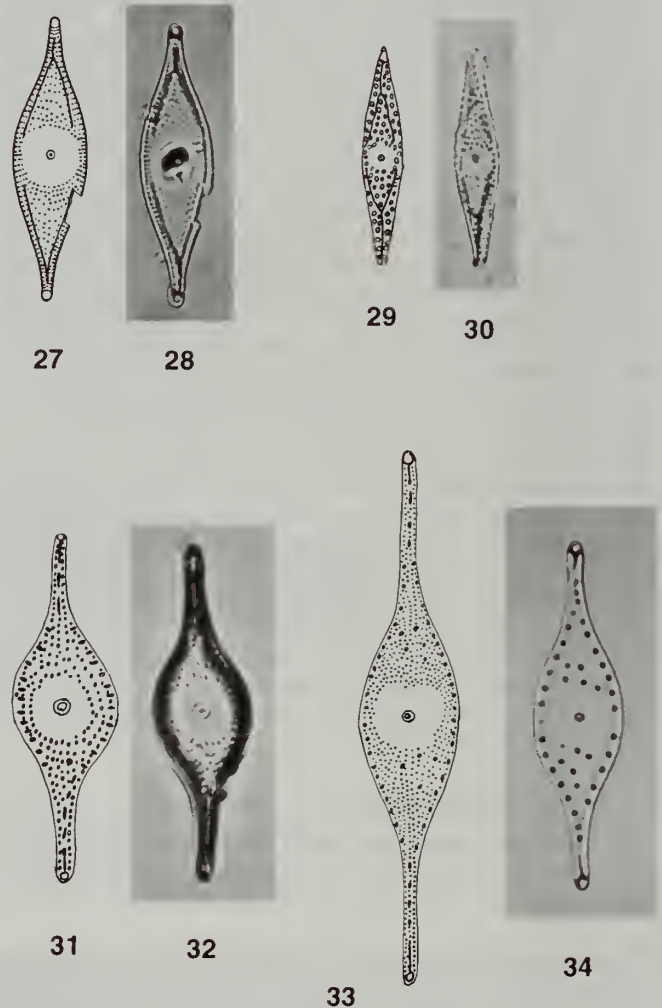
   Rutilaria minima subsp. *danica* R. Ross, from the Danish deposits dating from the Paleocene to Eocene boundary, was described and illustrated, but not named, by Homann (1991). It differs slightly from *R. minima* subsp. *minima* in outline and its areolae are larger and more widely spaced (compare Figs 27, 28 with Figs 29, 30). These differences are, however, too slight to justify separation at the specific level.

   The stem of the periplekton in *Rutilaria minima* and the other small species that occur in the Inza deposit is obviously much less robust than in other species of *Rutilaria*. As a consequence, most of the specimens consist either of a single valve or of a whole frustule with the stems of the periplekta broken through. In most species of the genus, the majority of fossil specimens consist of two sibling valves joined together by intact periplekta or single valves either with the periplek-ton and a fragment of the valve face of the sibling valve attached or with the centre torn out.

   Three small species of *Rutilaria* from the Paleocene of Ulyanovsk and Penza oblasts were described by Anisimova

(in Proshkina-Lavrenko et al., 1949), but their names are not validly published as there are no figures accompanying them. There can be very little doubt that they are based on specimens from the group of four species from Inza listed above, but, as the descriptions are not very detailed, one cannnot be certain to which species each name applies. However, the description of *R. longirostris* suggests strongly that it is based on *R. minima* subsp. *minima*; the distribution and spacing of the areolae is correct for that subspecies and there is no mention of spines.

   Homann (1991) cites *Rutilaria philippinarum* sensu Jousé (1979: pl. 3 fig. 7), non Cleve & Grove, as a possible synonym of *R. minima* subsp. *danica*. This is an error for which the poor quality of Jousé's figure is probably responsible. This figure is almost certainly of *R. briggeri* R. Ross. The marginal and superficial spines are not in sharp focus and the striae are not resolved, although there is an indication of their pres-

27   28   29   30

31   32   34

33

Figs 27–34   Figs 27–28: *Rutilaria minima* subsp. *minima*, valve view, × 1000, BM 36335, Inza, Ulyanovsk oblast, Russia, holotype. Figs 29–30: *Rutilaria minima* subsp. *danica*, valve view, × 1000, BM 82225, Knudeklint, Fur, Denmark, holotype. Figs 31–32: *Rutilaria areolata* subsp. *areolata*, valve view, × 1000, BM 77749, Totara, Oamaru, New Zealand. Figs 33–34: *Rutilaria areolata* subsp. *tenuior*, valve view, × 1000. Fig. 33: BM 78216, Chimborazo, Barbados; Fig. 34: valve view, BM 82239, Bermuda Rise, North Atlantic Ocean, holotype.

ence. It seems likely that Homann mistook the spines for areolae and thought that Jousé's specimens had areolae as coarse as those of her species.

Rutilaria minima subsp. *minima* is known only from the Paleocene deposit at Inza, Ulyanovsk oblast, Russia, but it probably occurs more widely in the Paleocene deposits in the central Volga basin. In the Inza deposit it is moderately frequent. The Fur-Formation, in which *R. minima* subsp. *danica* occurs, comes from about the boundary between the Paleocene and the Eocene (Homann, 1991). No species of *Rutilaria* had previously been recorded from this formation, except that Fenner (1988: 136) included '*Rutilaria bifurcata*' in a short list of species that commonly occur below 208 m core depth in a well at Harre, Salling, Denmark. I cannot trace any other mention of this name in the literature and it appears that it has not been validly published.

10. **Rutilaria areolata** Sheshukova-Poretskaya in Sheshukova-Poretskaya & Glezer in *Nov. Sist. Nizsh. Rast.* **1964**: 90, tabl. III fig. 5 (1964). – Glezer in *Trudy vses. nauchno-issled. geol. Inst.*, nov. ser. **130**: 73, tabl. V figs 3, 4 (1969); in Glezer et al., *Diatom. Vodor. SSSR* **1**: 129, tabl. XXXIII fig. 3 (1974). – Glezer & Sheshukova-Poretskaya in *Vest. Leningr. gos. Univ.* **1969**(9): 66, Tabl. 2 fig. 16 (1969). – Schrader & Fenner in *Initial Rep. deep Sea Drilling Proj.* **38**: 998, pl. 8 figs 11, 12, sed non pl. 37 fig. 16 (1976).

Rutilaria aff. *tenuicornis* sensu Fenner, *Diatoms in the Eocene and Oligocene sediments off NW–Africa, their stratigraphic and paleogeographic occurrences*: 125, pl. 29 fig. 10 (1981), non Grunow.

Rutilaria philippinarum sensu Desikachary & Sreelatha, *Oamaru Diatoms. Biblioth. Diatomol.* **19**: 225 (1989), pro parte, quoad pl. 96 fig. 6, non Cleve & Grove.

Frustules *c.* 8 μm deep. Valves with a slightly to moderately convex central portion, flat or slightly depressed at the centre, and with apical elevations rising abruptly from the valve face, 1.5–2 μm tall, 1.5–2 μm long; on the proximal side of each elevation a costa *c.* 1.5 μm long sloping down to the valve face, sometimes (? always) with transverse wing-like expansions from its upper edge; valves 23–80 μm long, 11–17 μm wide, with strongly convex margins to the central portion and narrow projections 2–4 μm wide. A marginal ridge *c.* 0.3 μm tall extending from elevation to elevation. Mantle vertical, *c.* 1–1.5 μm deep, hyaline except for a few small areolae on either side of the valve close to each apex. Central area circular, 4–9 μm in diameter. Areolae 0.2–0.6 μm in diameter, in radial striae at least on the central portion of the valve, striae 8–20 in 10 μm, areolae 6–20 in 10 μm. Periplekton with a circular stem 1.0–1.5 μm in diameter, very close to or touching that of the sibling valve; ring subcircular, 3.5–6 μm in diameter, flanged, clasping the stem of the sibling periplekton closely or, occasionally, loosely, the arms unequal, the shorter arm extending for *c.* 60°, the longer for *c.* 360°, its tip bent towards the valve from which it arises; line joining the centres of the stems of sibling periplekta on the apical axis. Ocelli 1–2 μm in diameter, transverse and inclined at 20°–30° to the vertical, the upper margin with 4 short rounded protrusions *c.* 0.3 μm broad and projecting *c.* 0.1 μm. Marginal spines *c.* 2 μm tall, those on the central portion of the valve blunt and with prominent tubercles on the outer side at the base, those on the projections pointed,

reaching to the apices but forming a single row on the projections, 4–7 in 10 μm, inset *c.* 1 μm from the margin of the valve face, the more distal ones with longitudinal costate extensions. Up to 8 superficial spines usually present on either side of the central area, on the distal part of the central portion of the valve.

subsp. **areolata**
Figs 31, 32, Plate VII (a)–(d).

Diameter of areolae 0.5–0.6 μm, velum consisting of three T-shaped volae. Striae 6–12 in 10 μm, areolae 6–10 in 10 μm.

[**Upper Cretaceous–Campanian**. Exposure XI(14) near Til'tim, basin of the river Synya, Tyumen'sk oblast, Russia (CAS 54041).]

Late Eocene. Chernigov, Ukraine (Glezer & Sheshukova-Poretskaya, 1969).
   Near Mialy on the River Irgiz, Kazakhstan, Russia (Glezer, 1969; in Glezer et al., 1974).
   Oamaru, Otago, New Zealand (BM 77749 Totara).

Late Eocene to early Oligocene. Left bank of the River Dnepra north of Dnepropetrovsk, Ukraine (Sheshukova-Poretskaya & Glezer, 1964).

Early Oligocene. Labrador Sea, North Atlantic, 53° 19.876'N, 45° 15.717'W, 3870 m depth. Ocean Drilling Program Hole 647A, 19R-1, 125–127 cm (BM SEM 70348–70357).

Late Oligocene. Vøring Plateau, Norwegian Sea, north Atlantic, 67° 47.11'N, 05° 23.26'E, 1297 m depth. Deep Sea Drilling Project Hole 338, 21-1, 67–68 cm, 21-2, 143–144 cm, 21 CC, 24-2, 108–109 cm (Schrader & Fenner, 1976).
   Coast of Morocco, North Atlantic, 26° 35.5'N, 14° 59.0' W, 1752 m depth. Deep Sea Drilling Project Hole 369A, 21-3, 68–69 cm (Fenner, 1981).

subsp. **tenuior** R. Ross, **subsp. nov.**
Figs 33, 34, Plate VII (e)–(g).

Areolae diametro 0.2–0.3 μm, velum ignotum, striae 14–20 in 10 μm, areolae 12–20 in 10 μm.

TYPUS. BM 82239, ex stratis eocaenicis de profundis maris Atlantici borealis.

Diameter of areolae 0.2–0.3 μm, velum unknown, striae 14–20 in 10 μm, areolae 12–20 in 10 μm.

Middle Eocene. Bermuda Rise, northern Atlantic Ocean, 30° 53.39'N, 67° 38.86'W, 5125 m depth. Deep Sea Drilling Project Hole 6, core 4–1, 127–133 cm (BM 82239 (holotype)).

Middle Eocene–late Oligocene. Barbados (BM SEM 72280–72289).
   Chimborazo, Barbados (BM 78216).

Late Eocene. Oamaru, Otago, New Zealand (BM 77754).

The most remarkable feature of *Rutilaria areolata* is the central longitudinal costa with wing-like lateral extensions that is attached to the proximal side of each elevation. These lateral extensions are not visible under the light microscope, but they are plainly seen on the scanning electron micrographs of *R. areolata* subsp. *tenuior* (Plate VII (e), (f)). The specimen of *R. areolata* subsp. *areolata* available for scanning electron microscopy is eroded but sufficient remains to show that it had the same structure (Plate VII (b), (d)). The two

subspecies differ only in the size of the areolae and their closeness, and this is not a sufficient basis for their separation at any higher level than subspecies. The differences between the two subspecies of *R. areolata* are almost identical to those between the two subspecies of *R. minima* R. Ross. In both species one subspecies has large areolae widely spaced whilst the other subspecies has smaller and closer areolae, but in *R. minima* the outline of the valve also differs slightly between the two subspecies. There are similarities between the two species also in the shape and size of the elevations and of the periplekton and it seems clear that they are closely related.

Rutilaria areolata also resembles *R. schenkii* in many ways. In particular, they are the only two species to have areolae on the mantle close to the apices but not elsewhere. *R. philippinarum* Cleve & Grove and *R. australis* R. Ross also have areolae on the mantle, but throughout its whole length.

Rutilaria areolata and *R. epsilon* Greville are the only two species to have protrusions along the upper rim of the ocellus (Plate VII (d), (f), Plate XIX (d)). They also both have tubercles on the outer side of the marginal spines at their bases (Plate VII (c), (g), Plate XIX (b)). Nevertheless they do not seem to be closely related. *R. epsilon* has much more in common with other species with tubercles on the marginal spines: *R. hustedtii* R. Ross, *R. barbadensis* R. Ross, *R. elliptica* Greville, *R. australis* R. Ross, *R. philippinarum* Cleve & Grove and *R. szakalensis* Pantocsek, none of which have costae on the distal part of their valves. *R. kamyshlovensis* R. Ross also has tubercles on the marginal spines but all its other characters indicate that it is not closely related to any of the other species with such tubercles. It would seem that these have evolved independently in three separate lineages.

Unfortunately, both subspecies of *Rutilaria areolata* are very rare in all the fossil deposits containing them that I have been able to study. In consequence, there is no information about the range of variation within any population, in particular whether the characters that distinguish the subspecies vary.

There is some overlap in the distribution of the two subspecies. One specimen only of each has been found in the Oamaru diatomite. The specimen of *Rutilaria areolata* subsp. *areolata* from that locality was misidentified as *R. philippinarum* Cleve & Grove by Desikachary & Sreelatha (1989). Elsewhere, *R. areolata* subsp. *tenuior* has been found in the middle Eocene from the Bermuda Rise in the North Atlantic and in the middle Eocene–Oligocene deposits on Barbados. *R. areolata* subsp. *areolata* is known from the upper Eocene of Kazakhstan, the upper Eocene to Oligocene boundary of the Ukraine, and from Oligocene core samples from the Norwegian and Labrador Seas and from just off the coast of Morocco. Schrader & Fenner (1976) also record *R. areolata* from the upper Oligocene of the Iceland–Faeroe ridge, but the specimen from there that they illustrate (pl. 37 fig. 16) is not *R. areolata* but an unnamed species discussed below as *Rutilaria* sp. B (p. 63). There is also a further record, unaccompanied by an illustration, of the occurrence of *R. areolata* in middle Eocene material recovered from Hole 206 of the Deep Sea Drilling Project in the Tasmanian Sea, South Pacific (Strel'nikova, 1988), but on which subspecies, if either, this is based is uncertain.

The record of *Rutilaria areolata* subsp. *areolata* from the upper Cretaceous is based on a selected specimen mounted by the late Mr A.L. Brigger, who labelled it as coming from exposure XI(14) near Til'tim in western Siberia, one of the sources of the Campanian material described by Strel'nikova

(1974). There is no doubt about the identity of the specimen, but there is about the locality. It is possible that it actually came from another sample from Russia. A number of such samples were sent by Dr A. Jousé to Dr Hanna, and passed on by him to Mr Brigger, whose recording of the locality of specimens and samples was often somewhat perfunctory. As Strel'nikova did not find any specimens of this taxon in her study of the material from Til'tim, and as there is no record of its occurrence between the Campanian and the upper Eocene, it seems very likely that the locality information on slide CAS 54041 is erroneous.

11. **Rutilaria schenkii** R. Ross, **sp. nov.**
Figs 35, 36, Plate VIII (a)–(f).

Valvae ad centrum parum depressae, elevationibus apicalibus *c.* 2 μm altis, 2–2.5 μm longis, costa ad 5 μm longa proximaliter affixa; valvae marginibus portionis centralis parallelis vel parum convexis, in projecturas decrescentes angustatae, 60–120 μm longae, 10–14 μm latae, projecturae 3.5–4 μm latae, decrescentes apices versus 2–3 μm latae esse; projecturae nonnumquam inaequaliter longae. Limbus ab fronte costa marginali minima separatus, *c.* 1.5 μm altus, verticalis, hyalinus praeter aream areolarum parvarum *c.* 3 μm × *c.* 1 μm prope apicem utrumque in alterutro latere valvae. Area centralis circularis, diametro 5.5–7.5 μm. Areolae diametro 0.5–0.75 μm, unaquaeque velo ex radiis angustis tribus ad centrum conjunctis constanti et prope superficiem externam valvae posito instructa, areae centrali oppositae in striis curtis radialibus vel singulariter in linea dispositae, alibi irregulares, 6–9 in 10 μm. Periplekton caule circulari diametro 1–1.5 μm, 6.5–7.5 μm alto, ad eum valvae fraternae appresso, annulo circulari diametro 5–8 μm margine alata, ex brachiis inaequalibus caulem periplekti fraternae non arcte amplectentibus constanti; brachia margine alata hiato litterae 'U' ad instar interrupta instructa; brachium brevius *c.* 120° extensum, brachium longius *c.* 270° extensum, fine deorsum deflexa et inter valvam et finem brachii longioris periplekti valvae fraternae inserta. Ocelli diametro 1.5–2 μm, transversi, ab verticali 45°–75° inclinati, porellis *c.* 60 in 10 μm. Spinae marginales areae centrali oppositae nonnumquam interruptae, in portione centrali valvae ab margine frontis *c.* 2 μm distantes, in projecturis in serie una centrali dispositae, tenues, acutae, 2–3 μm altae, 3–5 in 10 μm, eae plus distales costis longitudinalibus elevationibus conjunctis instructae. 1–3 spinae superficiales in parte distali utraque portionis centralis. Cingulum ex tribus minimum, verosimiliter quatuor, copulis constans; valvocopula parte interiori *c.* 0.7 μm alta, parte exteriori *c.* 2 μm alta, hyalina; copula II parte exteriori *c.* 2 μm alta, areolis in striis curtis advalvaribus instructa, areolae et striae *c.* 30 in 10 μm.

TYPUS. CAS 104089 ex stratis eocaenicis superioribus ad 'Cantua Creek, Fresno County, California, U.S.A.'

Valves slightly depressed at the centre and with rounded apical elevations *c.* 2 μm tall and 2–2.5 μm long, with a costa up to 5 μm long attached to their proximal side; valves 60–120 μm long, 10–14 μm wide, with a central portion with parallel or slightly convex margins tapering into projections 3.5–4 μm wide narrowing to 2–3 μm wide at the apices, the projections sometimes of unequal length. A slight hyaline marginal ridge less than 1 μm tall extending from elevation to elevation. Mantle vertical, *c.* 1.5 μm deep, hyaline except for an area *c.* 3 μm × *c.* 1 μm of small areolae just proximal to each apex

on either side of the valve. Central area circular, 5.5–7.5 μm in diameter. Areolae 0.5–0.75 μm in diameter, each with a velum near the outer surface of the valve consisting of three narrow spokes joining in the centre; areolae opposite the central area in short radial striae or in a single row, elsewhere irregular, 6–9 in 10 μm. Periplekton with a circular stem 1–1.5 μm in diameter, 6.5–7.5 μm tall, appressed to that of the sibling valve; ring circular, 5–8 μm in diameter, with a flange interrupted by a U-shaped gap, not closely clasping the stem of the sibling periplekton; the arms unequal, the shorter arm extending for *c.* 120°, the longer for c. 270°, its tip reflexed towards the valve and lying between it and the tip of the longer arm of the periplekton of the sibling valve. Ocelli 1.5–2 μm in diameter, transverse, inclined at 45°–75° to the vertical, poroids *c.* 60 in 10 μm. Marginal spines slender, pointed, 2–3 μm tall, sometimes interupted opposite the central area, 3–5 in 10 μm, inset *c.* 2 μm from the valve margin on the central portion of the valve, in a single central row on the projections, the most distal ones at either apex with longitudinal costae reaching the elevations. 1–3 superficial spines present on each distal part of the central portion. Mature cingulum consisting of at least three, probably four, copulae; valvocopula with a pars interior *c.* 0.7 μm deep and a pars exterior *c.* 2 μm deep, hyaline; copula II with a pars exterior *c.* 2 μm deep with areolae in short striae on the advalvar part, areolae and striae *c.* 30 in 10 μm.

Late Eocene. Bassendorf Shale, south end of Coos Bay, Coos County, Oregon, U.S.A., California Academy of Sciences sample no 1612, leg. H.G. Schenk (BM 82237, CAS 216044).

200–300 feet (60–90 m) below top of Lillis Shale, Cantua Creek, Fresno County, California, U.S.A. (BM 78204, SEM 97976–97985, 98041–98047, 98051: CAS 104089 (holotype)).

Rutilaria schenkii is known from only two localities, and only in small numbers from each of these. Of the thirteen specimens from the two localities that have been available for examination with the light microscope, there are eight in valve view, seven of them, including the holotype, single valves with the stem of the periplekton broken across and the ring missing. Only one is a sibling pair of valves with intact periplekta. There is also only one specimen consisting of a pair of sibling valves in girdle view. The remaining four specimens are lying obliquely. Several of these specimens have the projections broken through. Also four specimens from the type locality have been available for examination with the scanning electron microscope. One of these consists of a very immature frustule with two broken sibling valves attached (Plate VIII (d)). This is the only specimen seen with any elements of the girdle present and it provides only limited information about its morphology.

Rutilaria schenkii and *R. areolata* R. Ross subsp. *areolata* resemble each other closely. The spacing of their areolae is very similar and the areolae themselves are of comparable size, appearing larger than those of other species of comparable dimensions, except for *R. minima* var. *danica* R. Ross, which has no marginal spines. Both *R. schenkii* and *R. areolata* have a patch of small areolae on the mantle just proximal to each apex (Plate VIII (b)), and this is not present in any other species of *Rutilaria*. The differences between them, however, are more than those between *R. areolata* subsp. *areolata* and subsp. *tenuior*. Those only differ in the size and closeness of the areolae and in the size of the patches of areolae on the mantle close to the apices; in *R. areolata*

subsp. *tenuior* this may be reduced to a single areola. *R. schenkii*, however, differs from *R. areolata* in outline, in the larger diameter of the ring of its periplekton, in the shape of the apical elevations, in the absence of wings on the costae attached to the elevations, and in the presence of superficial spines. These differences are sufficient to justify separating the two taxa at specific rather than at subspecific level.

In *Rutilaria minima* R. Ross, although there are no marginal spines, there is a well developed costa in the position at which these spines occur in *R. schenkii*. Also the size and spacing of the areolae are very similar in *R. minima* subsp. *danica*, *R. areolata* subsp. *areolata* and *R. schenkii*, as are the periplekta of the three species. There are thus strong indications that the three are closely related. The two insufficiently known species of *Rutilaria* from the Oligocene of the Iceland-Faeroe ridge discussed below (p. 63) as *Rutilaria* sp. A and *Rutilaria* sp. B are also very close to *R. schenkii*, but *Rutilaria* sp. A has its marginal spines in two rows throughout and *Rutilaria* sp. B has a different outline and no costae attached to the proximal sides of the elevations. Until more specimens are available for examination, it will continue to be uncertain whether these two represent species distinct from *R. schenkii*.
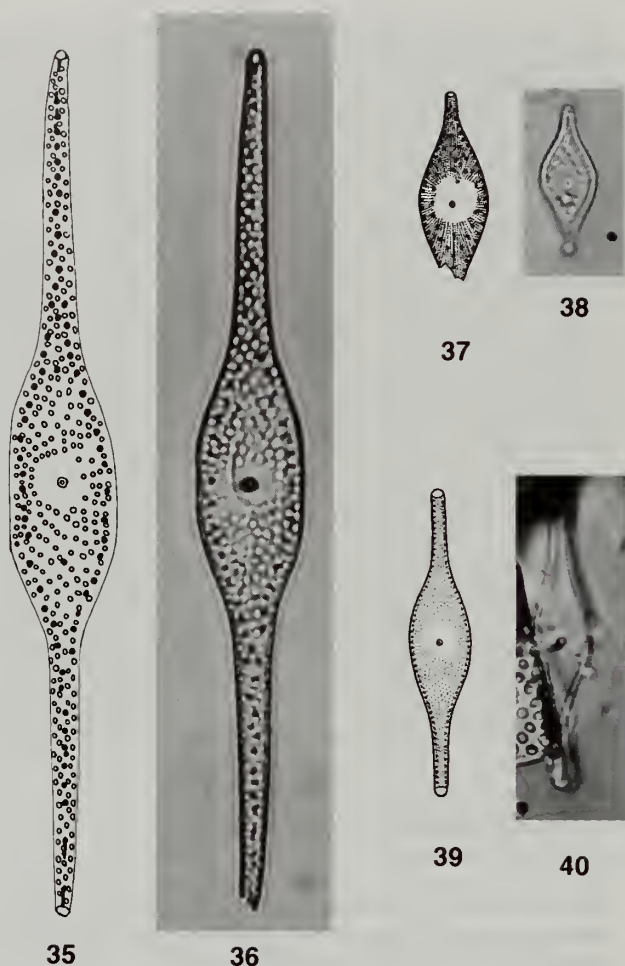
Rutilaria schenkii is known only from the upper Eocene of western North America. The species was first detected in a sample of the Bassendorf shale from Coos Bay, Oregon, collected by H.G. Schenk, and it is after him that the species is named.

12. **Rutilaria delicatula** R. Ross, **sp. nov.**
Figs 37, 38, Pl. IX(a)–(f).

? *Rutilaria tenuis* Anisomova in Proshkina-Lavrenko et. al., *Diatom. Analiz* 2: 215 (1949), nom. invalid., fossilis sine figura, non *R. tenuis* Grove & Sturt (1887).

Frustula 8–10 μm alta. Valva fronte parum convexa area centrali depressa et elevationibus rotundatis 1.2–1.5 μm altis et 1.75–2 μm longis instructa; valva portione centrali subcirculari vel elliptica in projecturas angustas decrescenti, 12–60 μm longa, 6.5–10 μm lata, projecturis 1.25–2 μm latis. Limbus ab fronte angulo separatus, verticalis, *c.* 0.5 μm altus, hyalinus. Area centralis circularis vel elliptica, diametro 2–5 μm. Areolae diametro *c.* 0.1 μm, in striis radialiter fasciculatis vel irregulariter dispositae, areolae et striae 22–30 in 10 μm. Periplekton caule circulari diametro 0.75–1 μm, 2.5–4 μm alto, ab eo valvae fraternae 0.75 μm distanti, annulo subcirculari diametro 4–6 μm, ex brachiis duobus inaequalibus constanti; brachium utrumque margine alata *c.* 1 μm lata in parte proximali, marginibus alatis hiato lato vadoso separatis, parte distali angusta, *c.* 0.5 μm lata, brachium brevius hamatum et *c.* 90° extensum, brachium longius *c.* 300° extensum et caule periplekti fraterni non arcte amplectens. Ocelli diametro 0.6–1 μm, transversi, ab verticali *c.* 45° inclinati, porellis *c.* 70 in 10 μm. Spinae marginales in seriebus duabus dispositae, eae in serie exteriore secus marginem frontis ab elevatione ad elevationem extensae, 8–12 in 10 μm, acutae, 0.3–0.5 μm altae, eae in serie interiore ab margine frontis 1.5–2 μm distantes, areae centrali oppositae interdum carentes, 6–9 in 10 μm, acutae, 0.75–1 μm altae. Spinae superficiales plerumque adsunt, 9 vel minus in latere utroque areae centralis dispersae. Cingulum ex copulis tribus constans; valvocopula parte interiori *c.* 0.3 μm alta et parte exteriori *c.* 3.5 μm alta, serie una vel seriebus duabus advalvaribus 20–30 in 10 μm ornata, alibi verrucosa; copula II

arm extending for *c.* 90° and hooked at the tip, the longer extending for *c.* 300°, its tip bent towards the valve from which it arises. Ocelli 0.6–1 μm in diameter, transverse, inclined at *c.* 45° to the vertical, porelli *c.* 70 in 10 μm. Marginal spines in two rows, the outer row pointed, 0.3–0.5 μm tall, along the margin from elevation to elevation, 8–12 in 10 μm, the inner row pointed, 0.75–1 μm tall, inset 1.5–2 μm, sometimes absent opposite the central area, 6–9 in 10 μm. Superficial spines usually present, nine or fewer scattered on either side of the central area. Cingulum consisting of three copulae; valvocopula with a pars interior *c.* 0.3 μm deep and a pars exterior *c.* 3.5 μm deep with one or two advalvar rows of areolae 20–30 in 10 μm, elsewhere verrucose; copula II with a pars exterior *c.* 1.5 μm deep, with three advalvar rows of areolae *c.* 40 in 10 μm; copula III with a pars exterior *c.* 0.5 μm deep with a single advalvar row of areolae *c.* 45 in 10 μm.

Paleocene. Inza, Ulyanovsk oblast, Russia. (BM 36335 (holotype), 36336, SEM 113298–113307, 113314–113319).

? Ulyanovsk oblast, Russia. (Proshkina-Lavrenko et al., 1949).

? Penza oblast, Russia. (Proshkina-Lavrenko et al., 1949).

The double row of marginal spines is the most distinctive feature of *Rutilaria delicatula*. There are two other species with double rows of marginal spines, *R. hyalina* R. Ross, also from Inza, and *R. briggeri* R. Ross, a much larger species known only from the middle and upper Eocene of the North Atlantic Ocean. In those two species, however, the marginal spines in the outer row are minute, visible only with the scanning electron microscope, whereas in *R. delicatula* the spines in the outer row are readily visible with the light microscope (Figs 37, 38). *R. delicatula* is also unusual in having fasciculate, rather than radial, striae (Fig 37, Plate IX (c), (d)). No other species of *Rutilaria* has striae arranged in this way.

Anisimova (in Proshkina-Lavrenko et al., 1949) published a description of a new species from the Paleocene of the Ulyanovsk and Penza oblasts in the central Volga basin, calling it *Rutilaria tenuis*. As this name of a new taxon of fossil plants was not accompanied by a figure, it is not validly published. Even if it had been, it would have been an illegitimate later homonym of *R. tenuis* Grove & Sturt (1887*a*). Glezer (in Glezer et al. 1974: tabl. XV fig. 14) provides a figure which she identifies as *Rutilaria tenuis* Anisimova. This clearly illustrates *Spinivinculum inzensis* R. Ross (1990). In Anisimova's description, however, there is said to be a thin, short process in the middle of the valve, which indicates that she was describing a *Rutilaria*, not a *Spinivinculum*. This species was most probably *R. delicatula*, the scattered puncta of her description being the superficial spines and the inner row of marginal spines, whilst the areolae, which are not easily seen, escaped her attention.

This is one of the small species of *Rutilaria* known so far only from the Paleocene deposits in the central Volga basin of Russia. It certainly occurs in the deposit of that age at Inza in Ulyanovsk oblast, in which it is more frequent than the other species of *Rutilaria* found there, *R. minima* R. Ross, *R. hyalina* R. Ross and *R. hustedtii* R. Ross. If my suggestion about the identity of *R. tenuis* Anisimova is correct, it also occurs in other deposits in Ulyanovsk and Penza oblasts.

13. **Rutilaria hyalina** R. Ross, **sp. nov.**
Figs 39, 40, Plate X (a)–(d).

Figs 35–40 Figs 35–36: *Rutilaria schenkii,* valve view, × 1000, CAS 104089, Cantua Creek, Fresno County, California, U.S.A., holotype. Figs 37–38: *Rutilaria delicatula*, valve view, × 1000, BM 36335, Inza, Ulyanovsk oblast, Russia. Fig. 38: holotype. Figs 39–40: *Rutilaria hyalina*, valve view, × 1000, BM 36335, Inza, Ulyanovsk oblast, Russia, holotype.

parte exteriori *c.* 1.5 μm alta, seriebus tribus advalvaribus areolarum *c.* 40 in 10 μm ornata; copula III parte exteriori *c.* 0.5 μm alta, serie una advalvari areolarum *c.* 45 in 10 μm ornata.

TYPUS. In BM 36335 ex stratis palaeocaenicis ad 'Inza, Ulyanovsk oblast,' Rossiam.

Frustules 8–10 μm deep. Valves with a slightly convex valve face, depressed at the centre, with rounded apical elevations 1.2–1.5 μm tall, 1.75–2 μm long; valves 12–60 μm long, 6.5–10 μm wide, with a sub-circular to elliptical central portion tapering into narrow projections 1.25–2 μm broad. Mantle separated from the valve face by a sharp angle, vertical, *c.* 0.5 μm deep, hyaline. Central area circular to elliptical, 2–5 μm in diameter. Areolae *c.* 0.1 μm in diameter, in radially fasciculate striae or irregularly arranged, areolae and striae 22–30 in 10 μm. Periplekton with a circular stem 0.75–1 μm in diameter, 2.5–4 μm tall, up to 0.75 μm from that of the sibling valve; ring sub-circular, 4–6 μm in diameter, not clasping the stem of the sibling periplekton closely, the arms unequal, each arm with a flange *c.* 1 μm wide on the proximal part, the flanges separated by a broad shallow gap, the distal part of the arms narrow, *c.* 0.5 μm wide, the shorter

Frustula *c.* 6 μm alta. Valva fronte fere plana, ad centrum parum depressa, elevationibus rotundatis 1–2 μm altis, 2.5–4.5 μm longis, instructa; valva portione centrali subcirculari vel elliptica in projecturas angustas decrescenti, 17–54 μm longa, 6–9 μm lata, projecturis 1–2 μm latis. Limbus verticalis, *c.* 0.5 μm altus, hyalinus. Area centralis circularis, diametro 3–4 μm. Areolae minutissimae, diametro *c.* 0.05 μm, in striis radialibus dispositae vel decussatae, areolae et striae 20–30 in 10 μm. Periplekton caule circulari diametro 0.5–0.75 μm, 3–5 μm alto, ab eo valvae fraternae *c.* 0.5 μm distanti, annulo diametro 5–6 μm ex brachiis duobus inaequalibus constanti; margine alata angusta in parte proximali brachii utriusque. Ocelli diametro *c.* 1 μm, transversi, ab verticali 10°–45° inclinati, porellis *c.* 70 in 10 μm. Spinae marginales in seriebus duabus, eae in serie exteriori minutae, globosae, secus marginem frontis ab elevatione ad elevationem extensae, *c.* 30 in 10 μm, per photomicroscopium invisibiles, eae in serie interiori cylindricae, 1.5–2 μm altae, ab margine frontis *c.* 0.5 μm distantes, ab elevatione ad elevationem extensae, 15–18 in 10 μm. Spinae superficiales nullae. Cingulum ex copulis duabus minimum constans; utraque copula *c.* 2 μm alta, serie una, hic illic seriebus duabus, areolarum *c.* 40 in 10 μm ornata.

Typus. In BM 36335 ex stratis palaeocaenicis ad 'Inza, Ulyanovsk oblast,' Rossiam.

Frustules *c.* 6 μm deep. Valves almost flat, slightly depressed at the centre and with rounded elevations 1–2 μm tall, 2.5–4.5 μm long; valves 17–54 μm long, 6–9 μm wide, with a sub-circular to elliptical central portion tapering into narrow projections 1–2 μm wide. Mantle vertical, *c.* 0.5 μm deep, hyaline. Central area circular, 3–4 μm in diameter. Areolae very small, *c.* 0.05 μm in diameter, in radial striae or decussate, areolae and striae 20–30 in 10 μm. Periplekton with a circular stem 0.5–0.75 μm in diameter, 3–5 μm tall, *c.* 0.5 μm distant from that of the sibling valve; ring 5–6 μm in diameter, with a narrow flange on the proximal part of each arm. Ocelli *c.* 1 μm in diameter, transverse, inclined at 10°–45° to the vertical, porelli *c.* 70 in 10 μm. Marginal spines in two rows; the outer row minute, globular, *c.* 30 in 10 μm, along the margin from elevation to elevation, not visible with the light microscope, the inner row cylindrical, 1.5–2 μm tall, 15–18 in 10 μm, inset *c.* 0.5 μm, extending from elevation to elevation. No superficial spines. Cingulum of two or more copulae *c.* 2 μm deep with one, or in places two, rows of areolae *c.* 40 in 10 μm.

Paleocene. Inza, Ulyanovsk oblast, Russia. (BM 36335 (holotype), 36336, SEM 113308–113313).

No specimen of *Rutilaria hyalina* in valve view with an intact periplekton has been seen. In consequence, a full description of the ring cannot be given. There are also no scanning electron micrographs giving clear pictures of the structure of the cingulum.

Rutilaria hyalina, like *R. delicatula* R. Ross and *R. briggeri* R. Ross, has two parallel rows of marginal spines (Plate X (c)). Those in the outer row are similar to those in *R. briggeri* in being so minute as to be invisible under the light microscope but differ from them in being globular, not pointed. Those in the inner row are cylindrical and without a terminal point (Plate X (c)). In all the other species of *Rutilaria* with marginal spines these are either pointed or expanded above; even the small spines in the outer row of *R. briggeri* are

pointed. Also, no other species has marginal spines as close as those in the inner row of *R. hyalina*, not even those in the outer row of *R. delicatula* or *R. briggeri*. The areolae of *R. hyalina* are also smaller than those in any other *Rutilaria* (Plate X (c)), and because of this they are not very visible under the light microscope, giving the valve the hyaline appearance that is indicated in the epithet chosen for the species.

Rutilaria hyalina has been found in only one fossil deposit, that from the Paleocene of Inza, Ulyanovsk oblast, Russia. It is comparatively rare in this deposit, being less frequent than any of the other three species found there, *R. minima* R. Ross, *R. delicatula* and *R. hustedtii* R. Ross.

14. **Rutilaria briggeri** R. Ross, **sp. nov.**
Figs 41, 42, Pl. XI(a)–(e).

? *Rutilaria philippinarum* sensu Jousé in *Beih. nov. Hedwigia* **64**: 440, pl. 3 fig. 7 (1979), non Cleve & Grove.

Valva fronte plana, ad centrum depressa, elevationibus apicalibus 1.5–2 μm altis, *c.* 3 μm longis instructa; valva portione centrali parum expansa ad apices 2–3 μm lata gradatim decrescens, 110–245 μm longa, 11–14 μm lata. Limbus verticalis, *c.* 3 μm altus, hyalinus, ab fronte costa marginali minima separatus. Area centralis circularis, diametro 8.5–10 μm. Areolae diametro *c.* 0.2 μm, in striis radialibus 18–21 in 10 μm, prope aream centralem crebrioribus quam alibi, dispositae; areolae 13–18 in 10 μm; striae areae centrali oppositae ex 2–4 areolis constantes. Periplekton caule circulari diametro 2–3 μm, 8–10 μm alto, ad eum valvae fraternae appresso, annulo circulari, diametro 10–12 μm, brachiis inaequalibus, margine alata hiato littera 'U' ad instar interrupta instructo; brachium brevius *c.* 150° extensum, brachium longius *c.* 330° extensum, caulem periplekti fraterni non arcte amplectens, parte distali angusta et deorsum deflexa. Ocelli diametro *c.* 1.25 μm, transversi, ab verticali *c.* 30° inclinati. Spinae marginales areae centrali oppositae plerumque carentes, in latere utroque valvae in seriebus duabus dispositae; eae in serie externa ab margine frontis *c.* 1 μm distantes, *c.* 10 in 10 μm, obtusae, *c.* 0.5 μm altae, ad fines distales seriei utraeque conjunctae et costam unam vel costas plures 5–25 μm longas formantes; eae in serie interna ab margine frontis *c.* 2 μm distantes, prope aream centralem 3–5 μm separatae, prope apices plus distantes et 7 μm separatae, acutae, 3–4 μm altae, eae plus distales in valvis longioribus in serie una centrali dispositae, interdum longitudinaliter extensae et costas formantes. 20 vel pauciores spinae superficiales, spinis marginalibus in serie interna similes, in utroque latere areae centralis.

Typus. BM 78189 ex stratis eocaenicis de profundis maris Atlantici borealis.

Valves flat, depressed at the centre, with apical elevations 1.5–2 μm tall, *c.* 3 μm long; valves 110–245 μm long, 11–14 μm wide, with a slightly inflated central portion tapering gradually to apices 2–3 μm wide. A slight hyaline marginal ridge less than 1 μm tall extending from elevation to elevation. Mantle vertical, *c.* 3 μm deep, hyaline. Central area circular, 8.5–10 μm in diameter. Areolae *c.* 0.2 μm in diameter, in radial striae 18–21 in 10 μm, closest near the central area, areolae 13–18 in 10 μm; striae opposite the central area of 2–4 areolae. Periplekton with a circular stem 2–3 μm in diameter, 8–10 μm tall, appressed to that of the

sibling valve; ring circular, 10–12 μm in diameter, with a broad flange interrupted by a 'U'-shaped gap between the two arms, not clasping the stem of the sibling periplekton closely, the arms unequal, the shorter arm extending for *c.* 150°, the longer for *c.* 330°, the tip of the longer arm narrow and deflected downwards; line joining the centres of the stems of sibling periplekta at *c.* 10° to the apical axis. Ocelli *c.* 1.25 μm in diameter, transverse, inclined at *c.* 30° to the vertical. Marginal spines usually absent opposite the central area, in two rows on either side of the valve; those in the outer row inset *c.* 1 μm from the margin of the valve face, *c.* 10 in 10 μm, blunt, *c.* 0.5 μm tall, uniting at the distal ends of each row to form one or more costae 5–25 μm long; those in the inner row inset *c.* 2 μm from the margin of the valve face, 3–5 μm apart near the central area, more distant and up to 7 μm apart close to the apices, pointed, 3–4 μm tall, the most distal ones on the longer valves in a single central row, sometimes extended longitudinally as costae. Up to 20 superficial spines on either side of the central area, similar to the marginal spines in the inner row.

Middle Eocene. Bermuda Rise, Atlantic Ocean, 30° 53.39′N, 67° 38.86′W, 5125 m depth. Deep Sea Drilling Project Hole 6, core 3–4, 72–78 cm (BM 78184, 78185, 78188, 78189 (holotype), 78190, 78191), core 4–1, 127–133 cm (BM SEM CB17.969–978, 15583–15587, 72250–72259), depth in hole unknown (BM SEM 1831, 1832, 1834; CAS 19041, 19042, 22067, 22068).

? Late Eocene. Mid-Atlantic Ridge, North Atlantic Ocean, 32° 19′N, 40° 00′W, 5117 m depth. Deep Sea Drilling Project Hole 387, core 9–3 (Jousé, 1979).

All the specimens of *Rutilaria briggeri* that have been available for examination are single valves or joined pairs of sibling valves. In consequence, there is no information about the frustule or girdle of this species.

The two rows of marginal spines in *Rutilaria briggeri* can be clearly seen in scanning electron micrographs (Plate XI (a), (c), (e)), but the outer row cannot be distinguished from areolae under the light microscope; only the costae formed by the fusion of the most distal ones can be seen. There are two other species of *Rutilaria* with two rows of marginal spines, both small species found in the Paleocene deposit at Inza in Russia. In *R. hyalina* R. Ross the spines in the outer row are even more minute than those in *R. briggeri* and are much closer, whilst those in the inner row are also much closer and are cylindrical, not pointed like those in *R. briggeri*. In *R. delicatula* R. Ross, the other species with two rows of marginal spines, the marginal spines in the outer row are much larger than those in *R. briggeri* and more like those in the inner row. This suggests that *R. briggeri* is probably more closely related to *R. hyalina* than it is to *R. delicatula*.

A second outer row of marginal spines may also be present in *Rutilaria cantabrigiensis* R. Ross and *R. flabellifera* R. Ross, neither of which have been examined with the scanning electron microscope. These two species are very similar to *R. briggeri* in outline, and *R. cantabrigiensis*, probably the evolutionary precursor of *R. flabellifera*, has equally close areolae arranged in radial striae. However, the structure of the periplekton in both *R. cantabrigiensis* and *R. flabellifera* is different from that in any other species of *Rutilaria*, although it might be derived from one in which the ring has a flange with a gap between the two arms, as is the case in *R. briggeri* (Plate XI (c), (e)).

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Figs 41–42 *Rutilaria briggeri*, valve view, × 1000, Bermuda Rise, North Atlantic Ocean. Fig. 41: BM 78189, holotype; Fig. 42: BM 78185.

Rutilaria lanceolata Grove & Sturt is another species that closely resembles *R. briggeri* in outline; the periplekton is also very similar to that of *R. briggeri*, and the areolae are similarly arranged, although more widely spaced. *R. lanceolata*, however, has no marginal spines.

Rutilaria tenuicornis Grunow and *R. tenuis* Grove & Sturt also have periplekta very similar to those of *R. briggeri,* and the density and arrangement of their areolae scarcely differs. Another point of resemblance between *R. tenuicornis* and *R. briggeri* is the fusion of their distal marginal spines to form

costae. Neither *R. tenuicornis* nor *R. tenuis*, however, has a second outer row of smaller marginal spines and in both the outline is different from that of *R. briggeri*, the central portion being very distinct from the projections.

Rutilaria briggeri occurs in the middle Eocene material recovered from Hole 6 of the Deep Sea Drilling Project situated in the area of the Bermuda Rise, and it is not known with certainty to occur anywhere else. It is uncommon but not rare in this material, which is contemporary with, and comes from the same general area as, that in which *R. cantabrigiensis* is found. Jousé's (1979) illustration of a specimen of *Rutilaria* from the upper Eocene of the mid-Atlantic ridge does not show sufficient detail for one to be certain that it is *R. briggeri*, but it resembles it more closely than it does any other species . It is certainly not *R. philippinarum* Cleve & Grove, the species with which Jousé identifies it.

15. **Rutilaria tenuicornis** Grunow in Van Heurck, *Syn. diatom. Belgique*: pl. 105 fig. 10 (1883). – Van Heurck, *Treat. Diatom.*, transl. Baxter: 433, fig. 156 (1896); *Traité Diatom.*: 433, fig. 156 (1899). – Coupin, *Album crypt., Alg.* **5**: pl. 314 fig. W (1922).

Rutilaria tulkii Castracane in *Rep. scient. Results Voy. Challenger, Bot.* **2**: 91, pl. 18 fig. 11 (1886).
Rutilaria edentula Castracane, *Rep. scient. Results Voy. Challenger, Bot.* **2**: 92, pl. 18 fig. 12 (1886). – Schütt in Engler & Prantl, *Nat. Pflanzenfam.* **1**(1b): fig. 176A (1896). – Okamura in *Rep. imp. Fish. Inst. Tokyo* **7**(4): 10, pl. 13 fig. 51 (1911). – Karsten in Engler & Prantl, *Nat. Pflanzenfam.*, 2. Aufl. **2**: 249, fig. 313A (1928).
Rutilaria epsilon var. *tenuicornis* (Grunow) De Toni, *Syll. alg.* **2**: 1021 (1894).
Rutilaria epsilon sensu Lefébure, *Atlas Déterm. Diatom.*: pl. 4 fig.6 (1947), non Greville. – Jurilj in *Acta bot. croat.* **24**: 77, fig. 11 (1965).

Valves depressed at the centre, elsewhere flat, with apical elevations 1.5–2 μm tall; valves 30–130 μm long, 10–19 μm wide, with an elliptical central portion tapering into projections that are sometimes very short. A slight hyaline marginal ridge less than 1 μm tall extending from elevation to elevation. Mantle vertical, 1.5–2 μm deep, hyaline. Central area circular, 9–11 μm in diameter. Areolae *c.* 0.3 μm in diameter, on the central portion in radial striae or irregularly arranged distally, on the projections in longitudinal striae, striae 18–26 in 10 μm, areolae 12–20 in 10 μm; striae opposite the central area of 1–5 areolae. Periplekton with a circular stem *c.* 2.5 μm in diameter, 5–8 μm tall, appressed to that of the sibling valve; ring circular, *c.* 9 μm in diameter, with a broad flange, interrupted by a broad and shallow gap between the two arms of the ring, not closely clasping the stem of the sibling periplekton, the arms unequal, the shorter extending for *c.* 150°, the longer for *c.* 330°, their overlapping tips narrow and the tip of the longer arm bent towards the valve from which it arises; the gap in the flange at *c.* 30° to the apical axis; line joining the centres of the stems of sibling periplekta at *c.* 30° to the apical axis. Ocelli 1–1.5 μm in diameter, transverse or slightly oblique, inclined at *c.* 30° to the vertical. Marginal spines pointed, *c.* 2.5 μm tall, 1.5–5 μm apart, occasionally even more widely spaced, never in a single central row on the projections, those on the projections, and often also those on the central portion, with bases extended longitudinally as short narrow costae, the costae immediately proximal to the

apices *c.* 5 μm long. 0–10 superficial spines on either side of the central area.

subsp. **tenuicornis**
Figs 43, 44, Plate XII (a)–(d).

Valve with a broadly elliptical to sub-circular central portion tapering sharply into projections with parallel sides; valves 30–130 μm long, 16–19 μm broad. Areolae in radial striae 18–20 in 10 μm, areolae 16–18 in 10 μm, the striae opposite the central area of (2–)4–5 areolae. The gap in the flange of the periplekton in the shape of a broad and shallow 'U'. Ocelli *c.* 1–5 μm in diameter. Marginal spines usually present opposite the central area, occasionally absent on the projections.

Late Pliocene. Road from Mantoep to Pelang, Java. Station 109M, Java Kaarteering-Sheet 109D (Lamongan) no. 83, East Java Horizon, Poetjangan layer (BM SEM 70101–70111; CAS 310041).

Middle Pleistocene. North side of mountain near Boetak, Java. BS–8, *Pithecanthropus* skull sample of Prof. Dubois (CAS 46059).

Recent. Makassar Strait, Indonesia (BM coll. Adams G382). Sulawesi, Indonesia (M. Voigt, personal communication). Philippines (US 3170, 3171).
Jolo, Sulu Archipelago, Philippines (US 3172).
Zamboanga, Mindanao, Philippines (Castracane, 1886).
Sulu Sea, Philippines. 8° 0′N, 121° 42′E, Challenger Station 211 (Castracane, 1886).
Manila, Philippines (BM 8859, 10905, 46239, 54316, coll. Adams GC2709; AWH coll. Van Heurck, s.n. (holotype); BRM H.t.46, N.d.47).
Tosa-wan, Shikoku, Japan (Okamura, 1911).

subsp. **paleogena** R. Ross, **subsp. nov.**
Figs 44, 46, Plate XII (e).

Rutilaria epsilon var. *longicornis* sensu Glezer & Sheshukova-Poretskaya in *Paleont. Sb. Lemberg* **5**: 122, tabl. II fig. 8a, b (1968), non (Brun & Tempère) A. Schmidt.

Valva portione centrali anguste elliptica in projecturas, interdum curtissimas et decrescentes interdum longiores et marginibus parallelis, gradatim angustatas; valvae 39–105 μm longae, 10–14 μm latae. Areolae in striis radialibus 18–26 in 10 μm, eis in portione centrali ad fines suas curvatis et margini valvae perpendicularibus; areolae 12–20 in 10 μm; striae areae centrali oppositae ex 1–4 areolis constantes. Hiatus in ala annuli periplekti latus, vadosus, litterae 'V' ad instar. Ocelli diametro *c.* 1 μm. Spinae marginales semper ad apices attingentes, aliquando areae centrali oppositae carentes.

TYPUS. CAS 104043, ex stratis eocaenicis ad 'Laguna Seca Creek, Merced County, California, U.S.A.'

Valve with a narrowly elliptical central portion tapering gradually into projections that are sometimes very short and tapering, sometimes longer and with parallel sides; valves 39–105 μm long, 10–14 μm broad. Areolae in radial striae 18–26 in 10 μm with those on the central portion curving to become perpendicular to the margin at their tips; areolae 12–20 in 10 μm; striae opposite the central area of 1–4 areolae. The gap in the flange of the periplekton in the shape

of a broad, shallow 'V'. Ocelli *c.* 1 μm in diameter. Marginal spines always extending to the apices, sometimes absent opposite the central area.

Middle Eocene. Antioch, Contra Costa County, California, U.S.A. (CAS 204046).

Laguna Seca Creek, Merced County, California, U.S.A. (CAS 104042, 104043 (holotype)).

Late Eocene. Near Dnepropetrovsk, Ukraine. (Glezer & Sheshukova-Poretskaya, 1968).

Dneiper–Dombas depression, Ukraine. (Ol'shtynskaya, personal communication).

Voronezh anticline, Voronezh oblast, Russia (Ol'shtynskaya, personal communication).

All the specimens of *Rutilaria tenuicornis* that I have seen have been either single valves or sibling pairs mounted in valve view and all have lacked any element of the girdle. I have seen only Californian specimens of *R. tenuicornis* subsp. *paleogena*. Two of these consist of single valves with the stem of the periplekton broken through; the third is a sibling pair with the periplekton obscured. The records from the Ukraine are based on the figures published by Glezer & Sheshukova-Poretskaya (1968), and a photomicrograph of one specimen and scanning electron micrographs of another, both with intact periplekta, kindly sent me by Dr Ol'shtynskaya. One of the scanning electron micrographs that she sent me is reproduced here as Plate XII (e).

The differences between the Eocene specimens from California and the Ukraine on the one hand and the late Pliocene to Recent ones from the north-eastern Indian Ocean and the western Pacific on the other are very minor and do not warrant separation at any level higher than subspecies. The two differ in outline, in the shape of the gap in the flange of the periplekton, and, to a minor extent, in the arrangement of the areolae (compare Figs 43, 44 and 45, 46). Their similarities in all other respects, and in particular in the possession of longitudinal costate extensions to their distal marginal spines and short costae immediately proximal to the elevations (Plate XII (c), (e)), show that the two taxa are so closely related that they can only be separated at subspecific level.

All of the published figures of *Rutilaria tenuicornis* subsp. *tenuicornis* are very inadequate; none show its large central area, although this is present on the holotype and on all the other specimens that I have seen. The illustration which accompanied the original publication of the name (Grunow in Van Heurck, 1883: pl. 105 fig. 10) depicts the areolae accurately in other respects, but in those illustrating the two synonyms published by Castracane (1886) the areolae are shown conventionally in two different styles, thereby concealing the fact that they are identically arranged. Okamura's (1911) figure shows no areolae at all. All the other figures are copies of one or another of these, even the ones given the name *R. epsilon* by Lefébure (1947) and Jurilj (1965), which are copies of Castracane's (1886: pl. 18 fig. 11) figure of *R. tulkii*. Even although it has not been possible to locate Castracane's type specimens, nor to see the original of Okamura's figure, one can be certain of what they depict. Comparison of specimens with such figures enables one to relate the conventional representations to the actual structure.

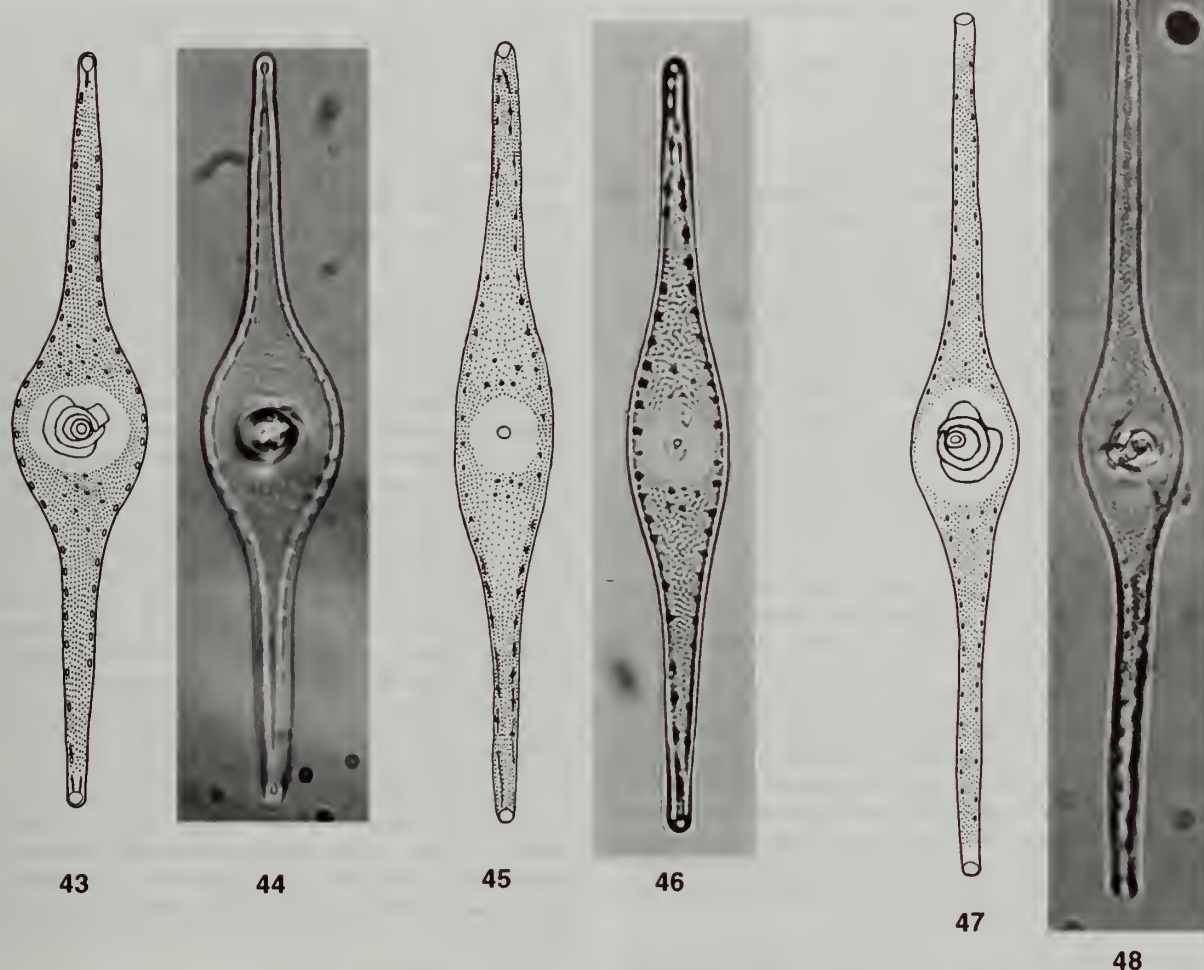*Rutilaria tenuicornis* subsp. *tenuicornis* is a somewhat variable taxon, in particular in the distribution of its marginal spines. The specimen on BM 8859 has its marginal spines only *c.* 1.3 μm apart and they are absent from most of the projections. This specimen nevertheless has two parallel longitudinal costae proximal to each elevation, although these are very poorly developed. Castracane's (1886) figure of *R. edentula* also shows a specimen in which the marginal spines are very close and are absent on the projections. On the other hand, BM 10905 (Figs 43, 44) and BM 54316, probably from the same gathering as BM 8859, have their marginal spines 3–5 μm apart, and they reach to the apices. The late Pliocene specimens of *R. tenuicornis* subsp. *tenuicornis* from Java differ from the recent ones by having no marginal spines opposite the central area and striae there of only 2 areolae (compare Fig 43 and Plate XII (b)). The marginal spines on the projections of the late Pliocene specimens are also much more widely spaced than those on any others. There is a similar difference between the Californian and the Ukrainian specimens of *R. tenuicornis* subsp. *paleogena*. In the Californian ones marginal spines are present opposite the central area and the striae there are of 3–4 areolae (Fig. 45); in the Ukrainian ones the marginal spines are absent opposite the central area and the striae there are of 1–2 areolae (Plate XII (e)). It will, however, only be possible to decide whether these slight differences between populations indicate that they are taxonomically separate when more specimens have become available.

Rutilaria tenuicornis subsp. *paleogena* and the contemporary *R. briggeri* R. Ross are similar in most respects. Their periplekta are almost identical, the spacing and arrangement of their areolae is similar, and both have distal marginal spines extended longitudinally as costae. Their outlines differ somewhat, and there is no outer row of very small marginal spines in *R. tenuicornis*. The latter difference makes it plain that the two are separate species, but the other resemblances suggest that they may be closely related, the outer row of small spines having been lost in the evolutionary development of *R. tenuicornis*.

Rutilaria tenuicornis and *R. tenuis* Grove & Sturt are also very similar in most respects, *R. tenuicornis* subsp. *tenuicornis* and *R. tenuis* having almost identical outlines. They are, however, separated by differences, set out below under *R. tenuis* (p. 40), that are greater than those which distinguish the two subspecies of *R. tenuicornis*.

Rutilaria tenuicornis subsp. *tenuicornis* is one of the only two taxa of *Rutilaria* known living today. It has an even more limited distribution than the other of these, *R. philippinarum* Cleve & Grove, being confined to the seas immediately around Indonesia, the Philippines and Japan. The gatherings of Recent material in which it has been found are either of plankton or of bottom mud. This indicates that its normal habitat is the neritic plankton, the specimens from bottom mud being dead frustules that have settled out of the water column. As a fossil it is known only from the upper Pliocene and Pleistocene of Java. The other subspecies is currently known only from the middle Eocene of California and the upper Eocene of the Ukraine, although a specimen from an upper Oligocene sample from off the coast of Morocco may also be this subspecies. The figure of this provided by Fenner (1981) does not show enough detail for identification (see p. 64). That no specimen with an age intermediate between those at which the two subspecies occur has been found demonstrates the extent to which the fossil record is incomplete.

Figs 43–48 Figs 43–44: *Rutilaria tenuicornis* subsp. *tenuicornis*, valve view, × 1000, BM 10905, Manila, Philippine Islands. Figs 45–46: *Rutilaria tenuicornis* subsp. *paleogena*, valve view, × 1000, CAS 104043, Laguna Seca Creek, Merced County, California, U.S.A., holotype. Figs 47–48: *Rutilaria tenuis*, valve view, × 1000, BM coll. Morley Jones s.n., Papakaiyo, Oamaru, New Zealand; different specimens on same selected slide.

16. **Rutilaria tenuis** Grove & Sturt in *J. Quekett microsc. Club*, ser. 2, **3**: 78, pl. 6 fig. 13 (1887). – Brun & Tempère in *Mém. Soc. Phys. Hist. nat. Genève* **30**(9): 54 (1889). Figs 47, 48, Plate XIII (a)–(d).

Rutilaria epsilon var. *tenuis* Grove & Sturt in *J. Quekett microsc. Club*, ser. 2, **3**: 74 (1887).
Rutilaria tenuicornis subsp. *tenuis* (Grove & Sturt) R. Ross in *Occ. Pap. Calif. Acad. Sci.* **123**: 24, pl. 1 fig. 6 (1976). – Desikachary & Sreelatha, *Oamaru Diatoms. Biblioth. Diatomol.* **19**: 226, pl. 96 figs 3, 4, 9 (1989).
Rutilaria sp. Tsumura in *Bull. Yokohama City Univ. Soc.* **16**, Nat. Sci. 1: 90, pl. 1 fig. 4 (1964). – Fenner in *Initial. Rep. deep Sea Drilling Proj.* **75**: 1265, pl. 2 fig. 6 (1984).

Valves depressed at the centre, elsewhere flat, with apical elevations sloping upward, 1.5–2 μm tall, 3–4 μm long; valves 75–220 μm long, 13–25 μm wide, with a broadly elliptical central portion tapering sharply into parallel-sided projections. A slight hyaline marginal ridge less than 1 μm tall extending from elevation to elevation. Mantle vertical, *c*. 1.5 μm deep, hyaline. Central area circular, 10–14 μm in diameter. Areolae *c*. 0.3 μm in diameter, occluded by domed vela,

in radial striae on the central portion and longitudinal striae, with the areolae irregularly decussate, on the projections, striae 15–20 in 10 μm, areolae 12–15 in 10 μm; striae opposite the central area of 1–3 areolae. Periplekton with a circular stem *c*. 2.5 μm in diameter, *c*. 10 μm tall, appressed to that of the sibling valve; ring circular, diameter 8–11 μm, with a broad flange, interrupted by a 'U'-shaped or wedge-shaped gap *c*. 3 μm × 3 μm between the two arms of the ring, not clasping the stem of the sibling periplekton closely, the arms unequal, one extending for *c*. 150°, the other for *c*. 330°, their overlapping tips narrow and deflected downwards; line joining the stems of sibling periplekta on the apical axis. Ocelli 1–2 μm in diameter, transverse, inclined at *c*. 30° to the vertical, porelli *c*. 50 in 10 μm. Marginal spines 3–4 μm tall, pointed, sloping distally near the apices, absent opposite the central area, spines 2–4 μm apart near the central area, more distant and up to 7 μm apart on the more distal parts of the projections, sometimes forming a single row on part of a projection. 2–6 superficial spines on either side of the central area, similar to the marginal spines.

Middle Eocene. Falkland Plateau, south-western Atlantic Ocean, 51° 08′S, 54° 22′W, 1525 m depth. Vema cruise 17,

core 107, 50 cm (CAS 216022˙, 216028, 216031, 216032, 216035), 175 cm (CAS 216034), level in core not noted (BM 78199, SEM CB14.164–168).

Rio Grande Rise, south-western Atlantic Ocean, 30° 0.25'S, 35° 33.59'W, 2086 m depth. Deep Sea Drilling Project Hole 357, core 24–5 (Fenner, 1984).

Late Eocene. Oamaru, Otago, New Zealand (BM 11154, 46635 (holotype), 52702, 52744, 52748, 64687, 68487 (= Tempère & Peragallo, Diatom. Monde ent., 141) Bain's Farm, 69161 (= Tempère & Peragallo, Diatom. Monde ent., no. 810) Troublesome Gully, 76863, 77752 Totara, 77754 Jackson's Paddock, 77757, 77758 Allan's Farm, 91026, coll. Adams TS271, coll. Morley Jones s.n. Papakaiyo, s.n. Papakaiyo, s.n. Papakaiyo, s.n. Jackson's Paddock; BRM H.t.47 Totara; CAS 126037 Totara, 134076, 139042 Totara; G, coll. Brun 141N; PC coll. Le Tourneur s.n.; US 7222 Flume Creek, 7223 Jackson's Farm, 7224 Jackson's Farm).

Early Oligocene. Falkland Plateau, south-western Atlantic Ocean, 51° 40'S, 48° 29'W, 2429 m depth. Vema cruise 18, core 112, 100 cm (CAS 216026).

All the specimens of *Rutilaria tenuis* that I have seen are mounted in valve view and all of them are without any part of the girdle. In consequence, no details of this can be given in the description.

The holotype of *Rutilaria tenuis*, the original of the figure included by Grove & Sturt (1887a) in the protologue of the species, is on the microscope slide BM 46635, originally in Sturt's collection. It is a sibling pair of valves inclined at c. 45° to one another, both valves having one projection broken off very close to its base. The figure represents one valve as complete, but this is an extrapolation by the artist, probably Sturt himself, on the assumption that specimens of this species are symmetrical about the centre.

Grove & Sturt (1887a) called this taxon 'R[utilaria]. epsilon var. tenuis' in their text (p. 74) and 'Rutilaria (epsilon var?) tenuis n.sp., Gr & St.' in the explanation of the plate on which it is figured (p. 78). The two names, *R. tenuis* and *R. epsilon* var. *tenuis*, must accordingly be regarded as simultaneously proposed alternative names for the same taxon published before 1 January 1953, and they are therefore both validly published. *R. tenuis* and *R. epsilon* Greville are distinct species and not even closely related; the areolae of *R. epsilon* are irregularly placed and are much more widely spaced than those of *R. tenuis*; also the ring of the periplekton of *R. epsilon* has a much less well defined flange and is of a very different shape from that of *R. tenuis*.

Brun & Tempère (1889) were unequivocal in treating *Rutilaria tenuis* and *R. epsilon* as distinct at the specific level. In a note following their descriptions of 'Rutilaria (Epsilon var. ?) capitata' and 'Rut. (Epsilon var. ?) longicornis' they write: 'Cette forme et la précédente nous paraissent devoir être considérées comme espèces et non comme de simples variétés. La *R. tenuis* Gr. & St. (Oamaru 6.13) a bien une forme analogue, mais elle offre une double striation oblique.' The 'double striation' to which Brun & Tempère refer is presumably the decussate arrangement of the areolae on the projections (Fig. 47, Pl. XIII(d)), which is represented in Grove & Sturt's figure as more regular than it actually is. Other authors, however, did not separate the two at the specific level. The specific name *R. tenuis* does not appear in

De Toni's (1894) *Sylloge Algarum*; he treated the taxon as *R. epsilon* var. *tenuis*. Mills (1934) and VanLandingham (1978) also omit the specific name *R. tenuis* from their catalogues of the names of diatoms, even although M. Peragallo (1903: 804) includes both the specific name and the varietal one, attributing both to Grove & Sturt.

Rutilaria tenuis is very similar to *R. tenuicornis* Grunow. Sturt originally did not distinguish them; he labelled the holotype of *R. tenuis* 'Rutilaria epsilon var. tenuicornis'. Grove, on the other hand, labelled a specimen mounted by him that is now in BM (BM 91026) as 'Rutilaria (epsilon v.) tenuis'. Like Sturt, I (Ross, 1976) considered *R. tenuicornis* and *R. tenuis* to be so close that they should be regarded as subspecies of one species. More detailed examination, however, has shown that the two taxa differ more considerably than I realized in 1976 and that separation at the specific level is appropriate. There are no longitudinal extensions at the base of the distal marginal spines and no costae just proximal to the apices in *R. tenuis* (Pl. XIII(d)). Also, the gap in the flange of the periplekton is as deep as it is broad in *R. tenuis* (Plate XIII (c)), whereas in *R. tenuicornis* it is broad and shallow (Plate XII (b)). The outline of the valve of *R. tenuis* is very similar to that of *R. tenuicornis* subsp. *tenuicornis* (compare Figs 47, 48 and 43, 44), but in that subspecies the marginal spines are normally not interrupted opposite the central area and the striae there are composed of 4–5 areolae. On the other hand, the european specimens of *R. tenuicornis* subsp. *paleogena* have the marginal spines interrupted opposite the central area and striae there of only 1–2 areolae, as in *R. tenuis*, but the two differ in the outline of the valve.

All the records of *Rutilaria tenuis* come from the middle Eocene to the early Oligocene of New Zealand or the south-western Atlantic. It is not common in any of the deposits in which it occurs, but it is more frequent than the other species of *Rutilaria* in the core samples from the Falkland Plateau.

17. **Rutilaria lanceolata** Grove & Sturt in *J. Quekett microsc. Club*, ser. 2, **2**: 324, pl. 18 fig. 6 (1886). – Desikachary & Sreelatha, *Oamaru Diatoms. Biblioth. Diatomol.* **19**: 225, pl. 96 figs 10, 11 (1989). – Reed in Edwards in *Paleont. Bull. Wellington* **64**: 144, pl. 8 figs 99, 100 (1991).
Figs 49, 50, Plate XIV (a)–(f).

Valves depressed in the centre, otherwise transapically convex, very slightly raised at the apices; valves 125–235 μm long, 12–14 μm wide, tapering gradually from a slightly inflated centre to rounded apices 2.5–3 μm wide. Mantle not sharply distinct from the valve face, hyaline. Central area circular, usually reaching to the margin of the valve face. Areolae 0.1–0.2 μm in diameter, in radial striae immediately distal to the central area, elsewhere more or less regularly decussate, striae and areolae 12–13 in 10 μm; areolae usually absent opposite the central area but occasionally a single row between the central area and the margin of the valve face. Periplekton with a circular stem c. 3 μm in diameter appressed to that of the sibling valve; ring circular, c. 10 μm in diameter, flanged, the flange with a slight indentation on the apical axis, not clasping the stem of the sibling periplekton closely, the arms unequal, one extending for c. 120° and tapering throughout, the other extending for c. 330° but the flange ending at c. 180°, beyond this the arm only c. 1 μm wide and bent towards the valve from which it arises. Ocelli c. 1.5 μm in diameter, transverse and inclined at c. 45° to the

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˙ The diatom collection at CAS has been re-numbered since 1976, and this is the specimen figured as Ross, 1976: pl. 1 fig. 6.

vertical. No marginal or superficial spines.

Late Eocene. Oamaru, Otago, New Zealand (BM 46612 (holotype), 64687, 74139 Totara, 76748 Jackson's Paddock, 77754 Jackson's Paddock, 77757, 91003, 91004, 91012, coll. Adams G80, coll. Morley Jones s.n. Allan's Farm, SEM CB9.152–156, CB9.344–347, 72687–72691, 72816–72818; BRM H.t.36 Totara, H.t.37 Totara; CAS 134077 Totara, 134078; G coll. Brun 45M Troublesome Gully, 141N).

Late Eocene to early Oligocene. Forrester's Hill, Oamaru, Otago, New Zealand (CAS 139038).

All the specimens of *Rutilaria lanceolata* that I have seen have been in valve view, and most of them have been single valves with the stem of the periplekton broken. This accounts for the deficiencies in the description. The holotype, BM 46612, was figured by Grove & Sturt (1886) as having the areolae arranged in transverse striae, but this was an error, as is shown by Fig. 50. Grove & Sturt's figure shows the broken periplekton as a small circle in the centre of the valve. Grunow (1887) was misled by their figure into suggesting that this species belonged not to *Rutilaria* but to *Synedra*, an opinion which he withdrew (Grunow, 1888) when he had seen a specimen.

The periplekton of *Rutilaria lanceolata* is very similar to that of *R. tenuicornis* Grunow, *R. tenuis* Grove & Sturt and *R. briggeri* R. Ross, and the arrangement and spacing of its areolae also resembles that found in those species. Whilst it differs from them in having no marginal or superficial spines, and not even any marginal ridge, it is nevertheless probably more closely related to them than to any other species.

All the known specimens of this species come from the upper Eocene to lowermost Oligocene deposit at Oamaru, New Zealand, where it is rare. It has been found nowhere else.

18. **Rutilaria cantabrigiensis** R. Ross, **sp. nov.**
Figs 51, 52.

Frustula 8–9 μm alta. Valvae ad centrum depressae, elevationibus apicalibus *c.* 2.5 μm longis et sursum acclivibus ad 1 μm altis, fronte alibi plana; valvae portione centrali anguste elliptica in projecturas angustatas gradatim decrescenti, 70–110 μm longae, 11–13 μm latae. Limbus ab fronte angulo separatus, *c.* 2 μm altus, verticalis, hyalinus. Area centralis circularis, diametro 8–10 μm. Areolae in striis radialibus dispositis, striae areolaeque *c.* 18 in 10 μm, striae areae centrali oppositae ex 2–3 areolis constantes. Periplekton caule circulari diametro 2 μm, 5–6 μm alto, ad eum valvae fraternae appresso, annulo *c.* 8 μm lato, brachiis subaequalibus apicibus suis non superpositis, periplekton valvae fraternae arcte amplectentibus, cauli periplekti valvae fraternae opposito extensionibus duabus exilibus *c.* 5 μm longis hiato litterae 'U' ad instar separatis et utraque ad 1–2 spinas superficiales in valvam fraternam attingenti et eas partim cingenti. Ocelli diametro 1.5–2 μm, transversi, ab verticali *c.* 15° inclinati. Spinae marginales in serie continua ab elevatione ad elevationem in utroque latere valvae, prope marginem frontis positae, acutae, 3–4 μm altae, in portione centrali valvae 4–5 in 10 μm, distaliter plus distantes. Costae duae *c.* 5 μm longae, *c.* 1 μm altae, ad elevationem utramque proximales adjacentesque et prope marginem utramque frontis positae. Spinae superficiales 1–3, spinarum marginalium similes, in latere utroque areae centralis. Valvocopula parte

exteriori *c.* 3 μm alta, serie singula areolarum *c.* 25 in 10 μm prope marginem advalvarem.

TYPUS. In BM 2866, ex stratis eocaenicis ad 'Cambridge, Barbados'.

Frustules 8–9 μm deep. Valves depressed at the centre, elsewhere flat, with apical elevations sloping upward, *c.* 1 μm tall, *c.* 2.5 μm long; valves 70–110 μm long, 11–13 μm wide, with a narrowly elliptical central portion tapering very gradually into tapering projections. Mantle separated from the valve face by a sharp angle, vertical, *c.* 2 μm deep, hyaline. Central area circular, 8–10 μm in diameter. Areolae in radial striae, striae and areolae *c.* 18 in 10 μm, the striae at the sides of the central area of 2–3 areolae. Periplekton with a circular stem 2 μm in diameter, 5–6 μm tall, appressed to that of the sibling valve; ring *c.* 8 μm across, the arms sub-equal and closely clasping the stem of the sibling periplekton, their tips not overlapping, the ring with two thin extensions on the side away from the stem of the sibling periplekton, one on either side of a U-shaped gap, extending *c.* 5 μm and reaching one or two superficial spines on the sibling valve and partially encircling these; line joining the centres of the stems of sibling periplekta at 5°–10° to the apical axis. Ocelli 1.5–2 μm in diameter, transverse, inclined at *c.* 15° to the vertical. Marginal spines pointed, 3–4 μm tall, in a continuous row from elevation to elevation on either side of the valve and situated close to the margin of the valve face, 4–5 in 10 μm on the central portion of the valve, more widely spaced distally. A costa *c.* 5 μm long and 1 μm tall on either side of the valve face immediately proximal to each elevation. 1–3 superficial spines on either side of the central area, similar to the marginal spines. Valvocopula with a pars exterior *c.* 3 μm deep and a single row of areolae *c.* 25 in 10 μm near the advalvar edge.

Middle Eocene. Cambridge, Barbados (BM 2863, 2866 (holotype), 3107, 3193, 3458).

Only five specimens of *Rutilaria cantabrigiensis* are known, and all of these are on strewn slides prepared by R.K. Greville in 1863–1865, with Canada balsam as the mountant and some with cover-glasses too thick for examination with oil-immersion objectives. Three of these specimens are pairs of sibling valves in valve view, the other two both consist of a frustule and two attached sibling valves in girdle view. It has, however, been impossible to give a full description of the cingulum because of the difficulty of examining the two in girdle view. Greville identified one specimen, that on BM 3107, as *R. ventricosa* Greville, a synonym of *R. elliptica* Greville; the others he identified to genus only.

The most remarkable feature of *Rutilaria cantabrigiensis* is the ring of its periplekton. Two thin extensions of this, separated by a U-shaped gap, reach beyond the central area as far as superficial spines on the sibling valve; these are partially encircled by indentations in the margins of the extensions of the ring (Figs 51, 52). The only other species with a periplekton similar to that of *R. cantabrigiensis* is *R. flabellifera* R. Ross, which also is known only from the Oceanic Beds of Barbados, but from a different locality, Conset Bay, in material that is almost certainly much younger (see p. 43 below). A number of other species of *Rutilaria* have thin flanges on the outer side of the rings of their periplekta, but these do not extend beyond the central area. In some of these species there is a U-shaped gap in the flange.
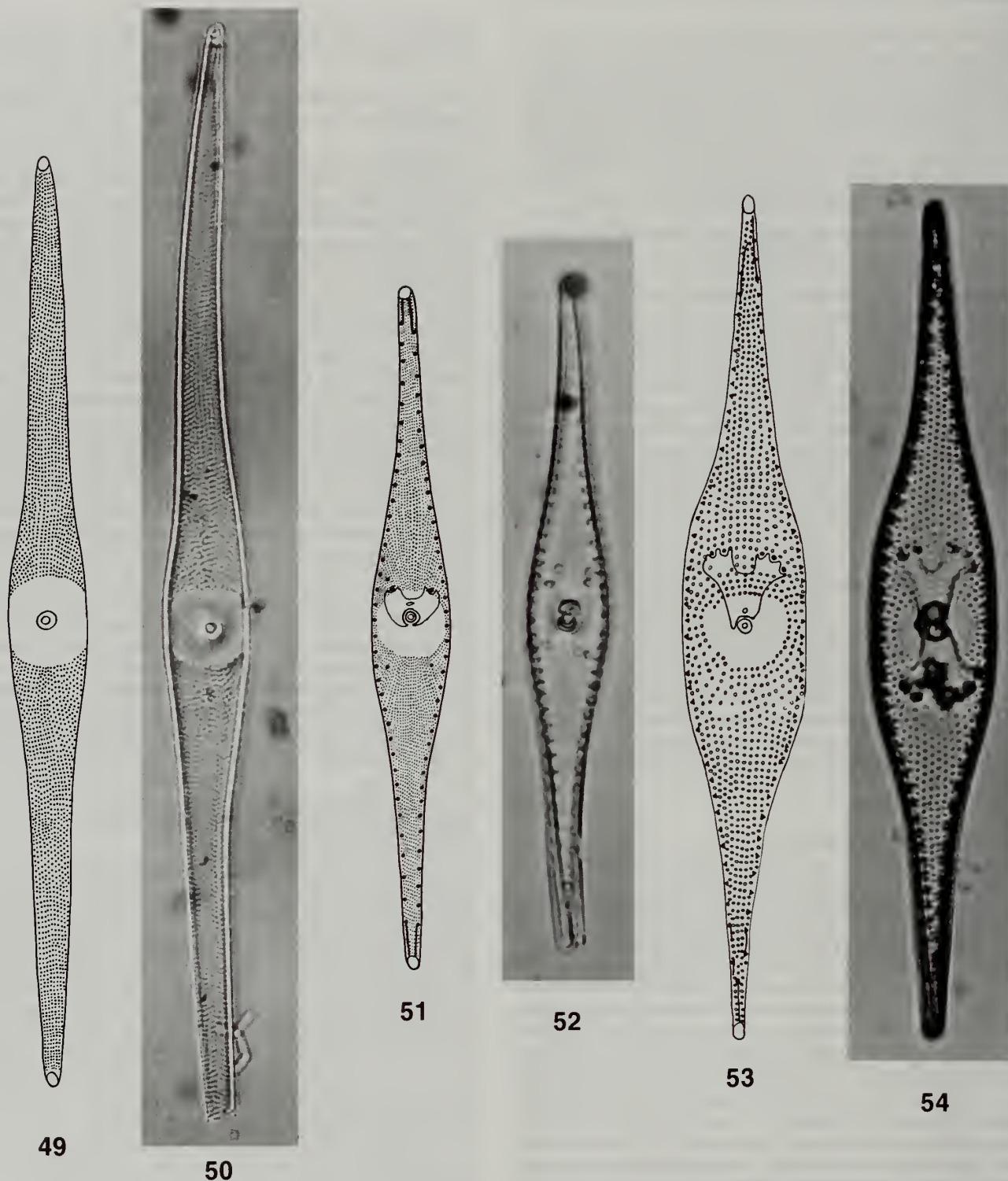
Figs 49–54 Figs 49–50: *Rutilaria lanceolata*, valve view, × 1000, Oamaru, New Zealand. Fig. 49: BM coll. Adams G80; Fig. 50: BM 46612, holotype. Figs 51–52: *Rutilaria cantabrigiensis*, valve view, × 1000, BM 2866, Cambridge, Barbados, holotype. Figs 53–54: *Rutilaria flabellifera*, valve view, × 1000, BM 78196, Conset, Barbados, holotype.

Amongst them are *R. tenuicornis* Grunow, *R. tenuis* Grove & Sturt and *R. briggeri* R. Ross, all of which also resemble *R. cantabrigiensis* and *R. flabellifera* in having elongate and slender valves and areolae in radial striae of similar density. This strongly suggests that there is a phylogenetic connection between all these species. The closest resemblance both in outline and in arrangement and density of the areolae is

between *R. cantabrigiensis* and *R. briggeri*. It is also possible that *R. cantabrigiensis* resembles *R. briggeri* in having a double row of marginal spines; if there were an outer row of small spines similar to those of *R. briggeri*, these would not be visible on the available specimens of *R. cantabrigiensis*.

All known specimens of *Rutilaria cantabrigiensis* come from the middle Eocene material from Cambridge, Barba-

dos, that was distributed by Christopher Johnson about 1860 or a little later. It is obviously rare in this deposit. The precise locality from which Christopher Johnson's samples came is not known (Robinson, 1941*b*). The finding of further specimens that will permit more detailed study of the species by, for instance, scanning electron microscopy can thus be only a matter of chance.

19. **Rutilaria flabellifera** R. Ross, **sp. nov.**
Figs 53, 54.

Valvae planae elevationibus apicalibus *c*. 3.5 μm longis et *c*. 1 μm altis; valvae portione centrali anguste elliptica in projecturas angustatas descrescenti, 138–220 μm longae, 20–24 μm latae, projecturis proximaliter 8 μm latis, ad apices 2.5 μm latis. Limbus ab fronte angulo et verosimiliter costa marginali minima separatus. Area centralis circularis, diametro 13–14 μm. Areolae diametro *c*. 0.5 μm, in striis radialibus 7–9 in 10 μm dispositae, areolae 5.5–7 in 10 μm. Periplekton caule circulari diametro 3.5 μm, ad eum valvae fraternae appresso, ad summum ejus brachium unum obtusum *c*. 90° circum caulem periplekti fraterni circumiens et extensio tenuis flabelli ad instar, ab periplekto fraterno procurrens, incisura centrali litterae 'U' ad instar et 5–6 incisuris minoribus spinas superficiales valvae fraternae partim cingentibus instructa; haec extensio 9–11 μm longa, *c*. 13 μm lata. Ocelli diametro 1.25–1.5 μm, transversi, ab verticali *c*. 45° inclinati. Spinae marginales ad apices fere vel admodum attingentes, 3–4.5 in 10 μm, prope marginem frontis in seriebus duabus ubique positae, acutae, una vel duae maxime proximales in costam curtam extensa; costa centralis vel costae parallelae duae ad utramque elevationem proximaliter affixa. 5–6 spinae superficiales prope aream centralem in latere quod versus extensio periplekti fraternae procurrit; in latere altero areae centralis spinae superficiales nullae.

TYPUS. BM 78196 ex stratis oligocaenicis miocaenicisve ad 'Conset, Barbados'.

Valves flat, with small apical elevations *c*. 1 μm tall and 3.5 μm long; valves 138–220 μm long, 20–24 μm wide, narrowly elliptical, tapering into projections that themselves taper to the apices, projections 8 μm wide proximally, tapering to 2.5 μm wide at the apices. A slight marginal ridge extending from elevation to elevation probably present. Mantle separated from the valve face by a sharp angle. Central area circular, 13–14 μm in diameter. Areolae *c*. 0.5 μm in diameter, in radial striae, striae 7–9 in 10 μm, areolae 5.5–7 in 10 μm. Periplekton with a circular stem 3.5 μm in diameter, appressed to that of the sibling valve, at its apex a blunt arm reaching *c*. 90° around the stem of the sibling periplekton and a fan-shaped flange projecting away from the sibling periplekton with a U-shaped central indentation and 5–6 smaller indentations partially surrounding superficial spines of the sibling valve; fan-shaped plate 9–11 μm in the apical direction, *c*. 13 μm wide; line joining the centres of the stems of sibling periplekta on the apical axis or at *c*. 5° to it. Ocelli 1.25–1.5 μm in diameter, transverse, inclined at *c*. 45° to the vertical. Marginal spines extending almost or quite to the apices, 3–4.5 in 10 μm, inserted close to the margin, in two rows throughout, pointed, the most distal one or two with short costate extensions; a central costa or two parallel costae proximal to each elevation. 5–6 superficial spines present near the central area on the side towards which the flange of

the periplekton of the sibling valve projects; no superficial spines on the other side of the central area.

Early Oligocene–early Miocene. Conset, Barbados (BM 78196 (holotype), 78214; CAS 28053, 142045).

All the four specimens of this species that I have seen are mounted on microscope slides in valve view. There is accordingly no information available about the cingulum nor any of the detail that the scanning electron microscope has provided for other species.

Rutilaria flabellifera resembles *R. cantabrigiensis* R. Ross in having a periplekton with a flange that extends away from the periplekton of the sibling valve as far as the superficial spines on that valve (Figs 53, 54). The two parts of this flange on either side of the U-shaped gap are both wider and longer than those in *R. cantabrigiensis*, but the reduction of the rest of the ring in *R. flabellifera* to no more than a short arm going only 90° around the stem of the sibling periplekton is an even greater difference between the two species. Sibling valves are nevertheless clearly held together; the specimens seen consist of sibling pairs. It appears that the distal edge of the flange of one valve grips superficial spines of the other, and this prevents their separation. *R. flabellifera* differs from *R. cantabrigiensis* not only in the shape of its periplekton but also by having larger and more widely spaced areolae and an outline with a somewhat more definite distinction between the central portion and the projections. There can be little doubt, however, that the one is phylogenetically descended from the other.

All the specimens of *Rutilaria flabellifera* were mounted by Brigger and labelled only 'Conset, Barbados.' The samples he had from there range from the middle Eocene to the early Miocene (pp. 8–9). The periplekton of *R. flabellifera* departs considerably more from that normal in *Rutilaria* than does that of *R. cantabrigiensis*. This indicates strongly that *R. flabellifera* is phylogenetically descended from *R. cantabrigiensis*, which occurs in the middle Eocene, and that it comes from one of the later samples from Conset, but whether this was lower Oligocene or lower Miocene is not known.

Rutilaria flabellifera also closely resembles *R. attenuata* R. Ross. Both have long and narrow valves, although *R. attenuata* is slimmer than *R. flabellifera* and is without any differentiation into central portion and projections; the projections of *R. flabellifera* are, however, not very distinct from the central portion, as Figs 53 and 54 show. The disposition of the areolae is also similar, although the striae of *R. attenuata* are rather closer than those of *R. flabellifera*. The exact structure of the periplekton of *R. attenuata* is not yet clear, but there are indications that it, also, is unusual. However, as *R. attenuata* has no superficial spines, it is unlikely to resemble that of *R. flabellifera*.

The epithet of this species is a noun in apposition, chosen because of the shape of the unusual periplekton; it is derived from flabellum, a fan, and means, literally, a female fan bearer, but also, by extension, since this was presumably one of their duties, a female slave.

20. **Rutilaria hustedtii** R. Ross, **sp. nov.**
Figs 55, 56, Plate XV (a), (b).

? *Rutilaria craspedostigma* Anisomova in Proshkina-Lavrenko et al., *Diatom. Analiz* **2**: 216 (1949), nom. invalid., fossilis sine figura.

Frustula 5–6 μm alta. Valva fronte leviter convexa, ad centrum leviter depressa, ab spinis marginalibus ad limbum declivi, elevationibus ad apices abrupte errigentibus, 1.0–2.25 μm altis et 1.25–1.5 μm longis. Valva portione centrali elliptica, in projecturas angustas, interdum curtissimas, gradatim decrescenti; valvae 19–50 μm longae, 7–9 μm latae, projecturis c. 1.5 μm latis. Limbus hyalinus, 1–1.5 μm altus, ab fronte costa marginali c. 0.2 μm alta separatus. Area centralis circularis, diametro 2.5–5 μm. Areolae diametro c. 0.15 μm, in fronte intra spinas marginales in striis radialibus plus minusve regularibus 18–20 in 10 μm, spinis marginalibus distales in striis regularibus 18–24 in 10 μm dispositae. Periplekton caule circulari diametro 0.75–1 μm, 2–4 μm alto, ad eum valvae fraternae appresso, annulo circulari, diametro 2.5 μm, brachiis paullo inaequalibus, margine alata hiato lato vadosoque inter brachia interrupta, instructo; brachium brevius c. 180° extensum, brachium longius paullo ulterius extensum. Ocelli diametro c. 1.25 μm, transversi, ab verticali c. 45° inclinati. Spinae marginales in serie una ab elevatione ad elevationem in utrumque latus frontis dispositae, ab margine frontis c. 1 μm distantes, acutae, unaquaque extus ad basim tuberculo instructa, 2–3 μm altae, 6–9 in 10 μm. Spinae superficiales nullae. Cingulum ex copulis duabus constans; valvocopula parte exteriori c. 3 μm alta, copula II parte exteriori c. 1.75 μm alta, copulae ambae serie una advalvari areolarum c. 36 in 10 μm et serie una abvalvari c. 40 in 10 μm.

Typus. In BM 36335 ex stratis palaeocaenicis ad 'Inza, Ulyanovsk oblast', Rossiam.

Frustule 5–6 μm deep. Valves with a slightly convex valve face, slightly depressed at the centre, sloping downwards from the marginal spines to the mantle, with elevations 1.0–2.25 μm tall and 1.25–1.5 μm long arising abruptly at the apices; valves 19–50 μm long, 7–9 μm wide, with an elliptical central portion tapering into narrow, sometimes very short, projections c. 1.5 μm wide. Mantle separated from the valve face by a marginal ridge c. 0.2 μm tall, vertical, 1–1.5 μm deep, hyaline. Central area circular, diameter 2.5–5 μm. Areolae c. 0.15 μm in diameter, on the valve face within the marginal spines in more or less regular radial striae 18–20 in 10 μm, distal to the marginal spines in regular striae 18–24 in 10 μm. Periplekton 2–4 μm tall, its stem circular and 0.75–1 μm in diameter, appressed to that of the sibling valve, ring circular, diameter 2.5 μm, with a flange interrupted by a broad, shallow gap between the two arms of the ring, the arms slightly unequal, the shorter extending c. 180°, the longer a little further. Ocelli c. 1.25 μm in diameter, transverse, inclined at c. 45° to the vertical. Marginal spines in a single row from elevation to elevation, inset c. 1 μm from the valve margin, pointed and with a tubercle on the outside at the base, 2–3 μm tall, 6–9 in 10 μm. No superficial spines. Cingulum of two copulae; valvocopula with a pars exterior c. 3 μm deep, copula II with a pars exterior c. 1.75 μm deep, both copulae with a single advalvar row of areolae c. 36 in 10 μm and a single abvalvar row c. 40 in 10 μm.

Paleocene. Inza, Ulyanovsk oblast, Russia (BM 36335 (holotype), 36336, SEM 113361, 113362).
   ? Ulyanovsk oblast, Russia (Proshkina-Lavrenko et al., 1949).

Rutilaria hustedtii is the only one of the species known from the Paleocene to have tubercles at the base of its marginal

spines (Plate XV (b)). The other species with such tubercles are *R. kamyshlovensis* R. Ross, *R. areolata* Sheshukova-Poretskaya, *R. barbadensis* R. Ross, *R. elliptica* Greville, *R. australis* R. Ross, *R. philippinarun* Cleve & Grove, *R. szakalensis* Pantocsek, and *R. epsilon* Greville. All of these, except for *R. kamyshlovensis* and *R. areolata*, form a closely related group, but those two species seem not to be related either to this group or to one another. *R. hustedtii* differs from *R. areolata* and resembles most of the other species with tubercles on the marginal spines in the distribution of its areolae and in the absence of distal costae. *R. kamyshlovensis* has very different periplekta and differently arranged areolae from any of the other species with tubercles on the marginal spines. However, *R. hustedtii* has periplekta (Plate XV (b)) very similar to those of *R. areolata* and *R. minima* R. Ross. It also resembles *R. minima* in size and in the outline of the valve and in the downward slope of the marginal zone of its valve face, but it differs in having marginal spines and two rows of areolae on each copula, not only one. Its affinities are thus by no means clear, although it seems most likely that it is, or is close to, the evolutionary precursor of the group consisting of *R. barbadensis*, *R. elliptica*, etc.

Anisimova's (in Proshkina-Lavrenko et al., 1949) description of *Rutilaria craspedostigma* gives such precise measurements for the length and breadth of the valve that it must have been based on a single specimen. Of the small species of *Rutilaria* found in the material from Inza, *R. hustedtii* is the one that the description most nearly fits, although Anisimova apparently saw no areolae on the specimen she described.

Rutilaria hustedtii has so far been found only in the Paleocene of the Volga basin, Russia, certainly from Inza, Ulyanovsk oblast, where it is much rarer than *R. minima* and *R. delicatula*, and possibly from other localities in Ulyanovsk and Penza oblasts. It is named after Dr F. Hustedt, through whose kindness I received the material containing it.

21. **Rutilaria barbadensis** R. Ross, **sp. nov.**
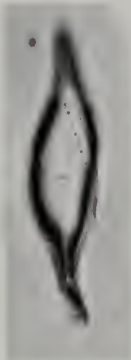Figs 57–59.

? *Rutilaria areolata* sensu Gladenkov in *Proc. Tenth Internat. Diatom Symp.*: 245 (1991), non Sheshukova-Poretskaya.

Valva portione centrali marginibus valde convexis; valvae 50–195 μm longae, 20–31 μm latae, valvae curtiores projecturis ad apices omnino gradatim descrentibus, valvae longiores projecturis subcapitatis 5 μm latis, ad apices expansis et 7–9 μm latis. Elevationes apicales minimae vel nullae. Costa marginalis exigua 0.5 μm maximum alta verisimiliter adest. Area centralis circularis, diametro 8–10 μm. Areolae diametro c. 0.3 μm, in portione centrali in striis radialibus 15–20 in 10 μm, in projecturis in striis longitudinalibus irregularibus c. 10 in 10 μm dispositae, areolis prope aream centralem 15–18 in 10 μm, in parte distali portionis centralis et in projecturis plus distantibus ad 7–9 in 10 μm. Periplekton caule circulari diametro 1.25–2 μm, ad eum valvae fraternae appresso, annulo subcirculari diametro 6–7 μm ex brachiis duobus inaequalibus periplekton valvae fraternae arcte amplectentibus constanti; brachium longius 270°–360°, id curtius 60°–180° extensum. Ocelli diametro c. 1.5 μm, ad axem transapicalem parum, ad verticalem c. 30°, inclinati. Spinae marginales ad apices plerumque attingentes, in projecturis nonnumquam absentes, in portione centrali valvae 2.5–6 in 10 μm, supra expansae atque intricatae et extus ad basim tuberculo parvo instructae, in projecturis plus remo-

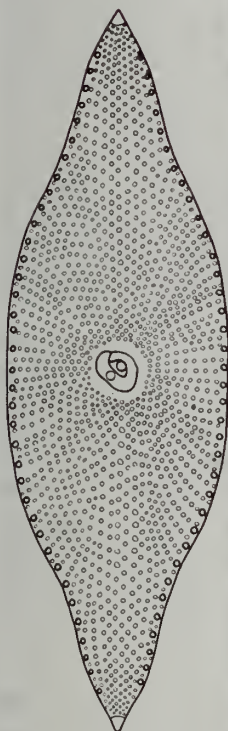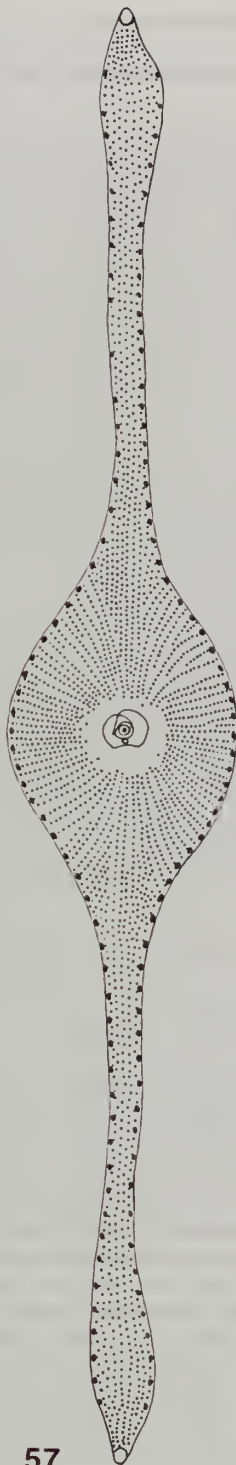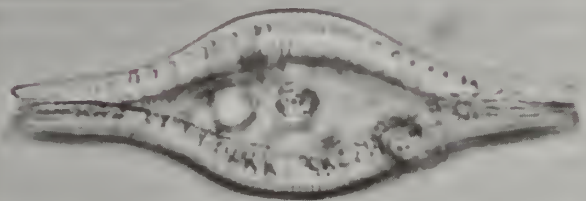**Figs 55–61** Figs 55–56: *Rutilaria hustedtii*, valve view, × 1000, BM 36335, Inza, Ulyanovsk oblast, Russia, holotype. Figs 57–59: *Rutilaria barbadensis*, valve view, × 1000. Figs 57, 58: BM 78203, Joe's River, Barbados, holotype; Fig. 59: BM 2765, Cambridge, Barbados. Figs 60–61: *Rutilaria elliptica*, valve view, × 1000, Cambridge, Barbados. Fig. 60: BM 3092; Fig. 61: BM 3281.

tae, tenuiores, acutae. Spinae superficiales nullae.

TYPUS. BM 78203, in stratis eocaenicis vel oligocaenicis ad 'Joe's River, Barbados'.

Valves with very slight or no elevations; valves 50–195 μm long, 20–31 μm wide, with a central portion with strongly convex margins, the shorter valves with projections that taper throughout to apices c. 2 μm wide, the longer valves with subcapitate projections 5 μm wide expanding to 7–9 μm wide at the apices. A slightly raised marginal ridge no more than 0.5 μm tall probably present. Central area circular, 8–10 μm in diameter. Areolae c. 0.3 μm in diameter, in radial striae 15–20 in 10 μm on the central portion and in irregular longitudinal striae c. 10 in 10 μm on the projections, areolae 15–18 in 10 μm near the central area, more widely spaced, to 7–9 in 10 μm, on the distal part of the central portion and on the projections. Periplekton with a circular stem 1.25–2 μm in diameter, appressed to that of the sibling valve; ring subcircular, 6–7 μm in diameter, clasping the stem of the sibling periplekton closely, the arms unequal, the shorter arm extending for 60°–180°, the longer arm for 270°–360°, its tip bent towards the valve from which it arises; line joining the centres of the stems of sibling periplekta on the apical axis. Ocelli c. 1.5 μm in diameter, slightly inclined to the transapical axis and inclined at c. 30° to the vertical. Marginal spines on the central portion expanded above and interlocking and with small tubercles on the outside at their bases, on the projections pointed and more slender, usually reaching to the apices but becoming more widely spaced towards these, sometimes absent on the projections, 2.5–6 in 10 μm. No superficial spines. The only girdle band seen open at one apex.

Middle Eocene. Cambridge, Barbados (BM 2765, 3036, 3114).

Late Eocene to early Oligocene boundary. Joe's River, Barbados (BM 78203 (holotype), 78217).

? **Late Oligocene.** Komandorsky Islands, Bering Sea (Gladenkov, 1991 and personal communication).

All the specimens of Rutilaria barbadensis that I have seen are mounted in valve view on slides for the light microscope; none have been available for scanning electron microscopy. There are three specimens from Cambridge, Barbados, and four from Joe's River, one of them no more than a girdle band detached from one of the other three. Those from Cambridge, which are of middle Eocene age, differ considerably in outline from those from Joe's River, which are later, from the Eocene to Oligocene boundary. The three from Cambridge are much shorter, 50 μm, 78 μm and 94 μm long, and have projections that taper throughout (Fig. 59), whilst those from Joe's River are longer, 120 μm, 123 μm and 193 μm, and have subcapitate apices to their projections (Figs 57, 58). This is their only difference, and the very small number of specimens seen from each locality means that the range of variation within the two populations is not known. One cannot tell whether they really differ in the outline of the valve, or whether the difference is only apparent and the result of chance. Such species as R. radiata Grove & Sturt and R. obesa Cleve have a range of variation in outline within a single population as wide as one that would encompass all the specimens included here within R. barbadensis (see Figs 19, 76).

Dr A. Yu. Gladenkov of the Institute of the Lithosphere, Moscow, has very kindly sent me photographs of the specimens on which he based his record (Gladenkov, 1991) of Rutilaria areolata Sheshukova-Poretskaya from the upper Oligocene of the Komandorsky Islands. These specimens are poorly preserved and somewhat obscured by dirt. Their outline is the same as that of the specimens of R. barbadensis from Joe's River, although they are slightly larger, 190–260 μm × 38–42 μm, but the width of their subcapitate projections and the diameter of their central area is similar. The areolae are in radial striae about 10 in 10 μm on the distal part of the central portion, the only place where they can be seen, and the marginal spines are about 2 in 10 μm. They thus agree with R. barbadensis in all the characters that can be distinguished, but are too poorly preserved and obscured by dirt for this identification to be certain.

Rutilaria barbadensis shares a number of characteristics with R. elliptica Greville, R. australis R. Ross, R. philippinarum Cleve & Grove, and R. szakalensis Pantocsek. All have periplekta with small rings the arms of which are unequal and without any flange, their marginal spines are expanded above and interlocking, and there are tubercles on the outside near the base of the marginal spines. Also, all five species have the areolae more widely spaced than the radial striae in which they are arranged, although in R. barbadensis this is only so on the projections and distal part of the central area and is less marked than in the other four species. It thus appears that all five are closely related. The Paleocene R. hustedtii also has tubercles on the outer side of its marginal spines at the base and probably either is, or is closely related to, an evolutionary precursor to this group of species

Rutilaria barbadensis is obviously rare in all the deposits in which it has been found. It is known with certainty only from the Oceanic Beds of Barbados in samples dating from the middle Eocene to the boundary between the late Eocene and the Oligocene, but it may also occur in the upper Oligocene of the Komandorsky Islands in the eastern Bering Sea.

22. **Rutilaria elliptica** Greville in Q. Jl microsc. Sci., new ser. **3**: 229, pl. 9 fig. 3 (1863); in Trans. microsc. Soc. Lond., new ser. **14**: 125, pl. 11 figs 9, 10 (1866). – De Toni, Syll. alg. **2**: 1022 (1894). – Schütt in Engler & Prantl, Nat. Pflanzenfam. **1**(1b): 100, fig. 176C (1896). – Coupin, Album crypt., Alg. **5**: pl. 314 fig. X (1922). – Karsten in Engler & Prantl, Nat. Pflanzenfam., 2 Aufl. **2**: 249, fig. 313C (1928). – Mills, Index Diatom.: 1424 (1934). – Williams in Bull. Br. Mus. nat. Hist. (Bot.) **18**: 46, pl. 53 fig. 4 (1988).

Figs 60, 61, Plate XVI (a)–(d).

Rutilaria ventricosa Greville in Q. Jl microsc. Sci., new ser. **3**: 228, pl. 9 fig. 2 (1863). – De Toni, Syll. alg. **2**: 1022 (1894). – Williams in Bull. Br. Mus. nat. Hist. (Bot.) **18**: 46 (1988).

Rutilaria superba Greville in Trans. microsc. Soc. Lond., new ser. **14**: 125, pl. 11 figs 11, 12 (1866). – De Toni, Syll. alg. **2**: 1022 (1894). – Schütt in Engler & Prantl, Nat. Pflanzenfam. **1**(1b): 100, fig. 176B (1896). – Coupin, Album crypt., Alg. **5**: pl. 314 fig. Y (1922). – Karsten in Engler & Prantl, Nat. Pflanzenfam., 2 Aufl. **2**: 249, fig. 313B (1928). – Williams in Bull. Br. Mus. nat. Hist. (Bot.) **18**: 46, pl. 53 fig. 11 (1988).

Rutilaria sp. J.D.Möller, Diatom.-Präp.: Taf. 16 supra, Reihe 6 no. 8 (1891); Verz. Lichtdrucktaf. Möll. Diat.-Präp.: 112 (1892).

Rutilaria ventricosa var. *rastellus* Brun in *Diatomiste*, **2**: 243, pl. 20 figs 4, 5 (1896). – Reinhold in *Verh. geol.-mijnb. Genoot., Geol. Ser.* **12**: 114, pl. 15 fig. 6 (1937).

Frustules rectangular, 12–14 μm deep. Valves not depressed at the centre, with elevations 1–3 μm tall sloping upwards to the apices. Valves 41–290 μm long, 21–40 μm wide, elliptical to lanceolate or with a central portion with moderately convex or parallel margins tapering into projections with cuneate apices, projections 7–11 μm wide and subcapitate to capitate in valves exceeding *c.* 100 μm in length. Mantle not sharply separated from the valve face, sloping slightly outwards, *c.* 3 μm deep, hyaline. Central area circular, 6–12 μm in diameter. Areolae 0.5–0.75 μm in diameter, in radial striae, striae 6–11 in 10 μm, areolae 4–6 in 10 μm, striae and areolae becoming closer near the apices. Periplekton with a circular stem 1.5–2 μm in diameter, *c.* 5 μm tall, normally close to or touching that of the sibling valve; ring small, subcircular, normally 6–10 μm in diameter, closely clasping the stem of the sibling periplekton, occasionally the ring up to 15 μm in diameter and not closely clasping the stem of the sibling periplekton, arms unequal, the shorter arm extending for 90°–180°, the longer for *c.* 300°, its tip bent towards the valve from which it arises; line joining the centres of the stems of sibling periplekta on the apical axis or inclined at no more than 10° to it. Ocelli 2.5–5 μm in diameter, slightly oblique to the apical axis and inclined at *c.* 10° to the vertical. Marginal spines on the central portion of the valve 8–12 μm tall, expanded above and interlocking and with small tubercles on the outside at the base, those on the projections or near the apices pointed and less tall, extending to the apices, *c.* 4 in 10 μm, inset *c.* 2 μm from the margin of the valve face. No superficial spines. Mature cingulum consisting of three copulae; valvocopula with a pars exterior 4–7 μm deep, indented at one apex; copula II with a pars exterior *c.* 5 μm deep and a small ligula; copula III with a pars exterior *c.* 3 μm deep; all copulae with vertical striae 14–20 in 10 μm.

Middle Eocene. Cambridge, Barbados (BM 2756 (holotype of *Rutilaria elliptica*), 2761, 2775, 2789, 2799, 2801, 2827, 2975, 3079, 3092, 3099, 3121, 3187, 3189, 3205, 3245, 3264, 3281, 3284, 3419, 3427 (lectotype of *Rutilaria superba*), 3434, 3451, 3460, 3463, 3472, 13669, 66928 (holotype of *Rutilaria ventricosa*), 67374a, 67452, 67553, 82240).

Middle Eocene–late Oligocene. Barbados (BM SEM 72269, 72272–72279, 104732–104735; PH coll. Febiger 158, coll. Shulze arr. 1264).

  Chimborazo, Barbados (G coll. Brun 4171).
  Clealand, Barbados (Brun, 1896).
  Mount Hillaby, Barbados (G coll. Brun 4128 (holotype of *Rutilaria ventricosa* var. *rastellus*)).

Late Eocene to early Oligocene. Joe's River, Barbados (BM 78215; CAS 31069, 43037, 142046).

Early Oligocene. Burnt Hill, Conset, Barbados (BM coll. Adams L122).

Early Miocene. Jérémie, Haiti (PH coll. Boyer E-6-25; Möller, 1891, 1892).

Middle Miocene. Goenong Gamping, near Nanggoelang, Java (CAS 48046; HAA REI AN9-24).

In *Rutilaria elliptica* there are very considerable changes in outline with change in length, the shortest specimens being elliptical to lanceolate, the longest having long capitate projections (Figs 60, 61, Plate XVI (c) and Williams, 1988: pl. 53 fig. 11). These differences in outline between specimens caused Greville to consider that they represented three different species. However, examination of a large number of specimens shows that they form a continuous series. Mills (1934: 1424) was the first to recognize that the two names published simultaneously by Greville, *R. elliptica* and *R. ventricosa*, referred to the same species; he chose *R. elliptica* as the name to be adopted, and his choice must be followed. That *R. superba*, based on specimens with long, subcapitate projections, also applied to the same taxon has not been recognized until now, but this is clear when a long series of specimens is examined. The range in outline is as wide as that in *R. radiata* Grove & Sturt (Fig. 19) and *R. obesa* Cleve (Fig. 76).

The specimens that are the originals of Greville's figures of both *Rutilaria elliptica* and *R. superba* are in his collection, his slide number and the location of the specimen on the slide being indicated on his original pencil drawing. In his protologue of *R. elliptica* (Greville, 1863) he illustrated one specimen only and this (BM 2756) is accordingly the holotype; it is illustrated also by Williams (1988: pl. 53 fig. 4). The originals of the two figures that he later provided under this specific name are BM 2789 (original of Greville, 1866: pl. 11 fig. 9) and BM 3434 (original of Greville, 1866: pl. 11 fig. 10). He included two illustrations in his protologue of *R. superba*, the originals of which are accordingly syntypes; I here designate BM 3427, the original of Greville, 1866: pl. 11 fig. 12, and also illustrated by Williams (1988: pl. 53 fig. 11), as the lectotype of this name. The other syntype, the original of Greville, 1866: pl. 11 fig. 11, is BM 2761. Greville's original drawing of *R. ventricosa* on the other hand is annotated 'Ralfs' slide'. BM 66928 is a slide of material from Cambridge, Barbados, mounted by Ralfs and with an indication of the position on it of a specimen identified by him as *Rutilaria* without any specific epithet. This specimen matches very closely Greville's illustration of *R. ventricosa* accompanying his first description of that species (Greville 1863: pl. 9 fig. 2) and is clearly the original of that figure; it is thus the holotype. This specimen is about 100 μm long and is slightly aberrant in that the marginal spines are absent for about 12 μm from one apex although they reach to the other. Only in this respect does it differ from the other specimens of *R. elliptica*, and there can be no doubt that it belongs to that species.

The specimens on BM 3264 and BM 3419 that I have identified as *Rutilaria elliptica* both come from Cambridge, Barbados, and each consists of a sibling pair of valves in girdle view. They are only 44 μm and 41 μm long respectively, distinctly shorter than all the other specimens of the species, the shortest of which is 56 μm long. Their periplekta are unusual; the stems are not close but separated by 3 μm and 8 μm respectively and their rings are 11 μm and 15 μm in diameter respectively. Also, the marginal spines of both are pointed throughout; the central ones are not expanded above and interlocking. Two other specimens have periplekta with rings larger than is usual for *R. elliptica*. The specimen on CAS 31069 from Joe's River, Barbados, has the rings of the periplekta about 11 μm in diameter and a gap of about 3 μm between their stems. This specimen, however, is not particularly short; it is 95 μm long with unusually broad projections about 17 μm wide tapering slightly to rounded apices. One of the two specimens from Chimborazo, Barbados, on coll.

Brun 4171 at G, that mounted in valve view, has a ring that is 15 μm × 13.5 μm. This, too, is not short but is about 80 μm long. It is not possible to see whether the central marginal spines of either of these specimens mounted in valve view are pointed or expanded above. In all other respects these four specimens have the characters of *R. elliptica*. Whether they are no more than slightly abnormal individuals of that taxon or whether their unusual characters indicate some taxonomic separation will only become apparent when more material is available.

Brun (1896) distinguished *Rutilaria ventricosa* var. *rastellus* by the presence of a small round tubercle at the base of each marginal spine. This character is, however, present in all specimens of the species and examination of the type specimen of this variety showed that it has no characters that distinguish it from other specimens of *R. elliptica*. I have also been able to examine the specimen from Java that Reinhold (1937) identified as Brun's variety and found that it too undoubtedly belongs to this species.

Rutilaria elliptica and *R. philippinarum* Cleve & Grove are very similar; they have the same range of outline, very similar periplekta, a very similar distribution of areolae on the valve face and very similar girdles. They differ, however, in a number of ways: marginal spines are present almost to the apices in *R. elliptica* but are absent from the distal parts of the valve in *R. philippinarum*, which has superficial spines not present in *R. elliptica*; *R. elliptica* has small elevations at each apex whilst *R. philippinarum* has none; there are areolae in short vertical striae on the mantle of *R. philippinarum* whereas the mantle of *R. elliptica* is hyaline. *R. australis* R. Ross is another very similar species which differs from *R. elliptica* in having vertical striae on the mantle and narrower projections that are never subcapitate.

Möller (1891) illustrated a very large specimen from Jérémie, Haiti. This is 290 μm long and 40 μm wide with each projection 110 μm long, 10 μm wide at its narrowest but expanding to 30 μm wide close to the apices. The largest specimen of *R. elliptica* that I have seen, one from Cambridge, Barbados, is 240 μm long, 27 μm wide, with projections 75 μm long and 8 μm wide, expanding to 12 μm wide near the apices. The magnification of Möller's photomicrograph is too small for details of the size and arrangement of the areolae to be distinguished, but it can be seen that marginal spines are present throughout the length of the valve. This, together with the outline of the specimen, makes it clear that it is *R. elliptica*. I have also seen one specimen from Jérémie, (PH coll. Boyer E-6-25) which has the apices broken off. Its projections are very narrow, only 3 μm wide, but it has all the other characters of *R. elliptica* and almost certainly belongs to that species, although there is a remote possibility that it is *R. australis*, a species from the middle and late Eocene of the southern hemisphere.

Rutilaria elliptica occurs in the Caribbean from the middle Eocene until the early Miocene. The only other place where it has been found is in the Wonosari series deposits of Java, which are of middle Miocene age.

A number of records of *Rutilaria elliptica* or one of its synonyms in the literature are based on misidentifications. Pantocsek's records of *R. ventricosa* from the Miocene of Nográdszakál (Szakal) in Hungary (1886) and Velky Krtis (Nagy-Kürtös) in Slovakia (1889) are based on specimens of *R. philippinarum*. Möller (1891, 1892) identified specimens of *R. radiata* Grove & Sturt from the late Eocene of Oamaru, New Zealand, as *R. superba*. Laporte & Lefébure (1930)

applied the name *R. elliptica* to a specimen of *R. obesa* Cleve, although they at the same time correctly identified another specimen of that species as *R. hexagona*, a synonym of *R. obesa*. Greville himself identified specimens of *R. barbadensis* R. Ross and *R. cantabrigiensis* R. Ross from Cambridge, Barbados, as *R. ventricosa*, but these misidentifications are not the basis of any published record.

23. **Rutilaria australis** R. Ross, **sp. nov.**
Figs 62, 63.

Rutilaria sp. Schrader in *Beih. Nova Hedwigia* **28**: pl. 10 fig. 19 (1969).
Rutilaria philippinarum sensu R. Ross in *Occ. Pap. Calif. Acad. Sci.* **123**: 23, pl. 1 fig. 5 (1976), non Cleve & Grove. – Desikachary & Sreelatha, *Oamaru Diatoms. Biblioth. Diatomol.* **19**: 225 (1989), pro parte, quoad pl. 96 figs 2, 5, 8.

Valvae ad centrum depressae, alibi planae, elevationibus *c*. 1 μm altis et *c*. 3 μm longis apices versus acclivibus, portione centrali elliptica in projecturas angustas, ad apices rotundatas, decrescentes, 65–125 μm longae, 21–31 μm latae, projecturae 3–4.5 μm latae. Limbus ab fronte angulo separatus, parum extrorsus declivis, 4–5 μm altus, striis verticalibus 7–8 in 10 μm fere ad marginem attingentibus instructus. Area centralis subcircularis, diametro 10–13 μm. Areolae diametro *c*. 0.3 μm, in fronte in striis radialibus dispositae, striae 6–10 in 10 μm, areolae 4–6 in 10 μm, sed striae areolaeque juxta aream centralem et prope apices plus contiguae. Periplekton caule circulari diametro 1.75–2.5 μm, *c*. 6 μm alto, ei valvae fraternae propinquo, annulo parvo, subcirculari, diametro 6–7.5 μm, periplekton valvae fraternae arcte amplectenti, brachiis inaequalibus; brachium brevius *c*. 180° extensum, brachium longius *c*. 300° extensum parte distali deorsum deflexa. Ocelli elliptici, *c*. 1.5 μm lati, 3 μm alti, transversi, ab verticali 10°–15° inclinati. Spinae marginales ad apices attingentes, 4–5 in 10 μm, in portione centrali valvae *c*. 6 μm altae, supra expansae atque intricatae et ad basim tuberculo parvo externo instructae. Spinae superficiales nullae.

TYPUS. In BM coll. Adams G639, ex stratis eocaenicis ad 'Jackson's Paddock, Oamaru, Otago' Novam Zelandiam.

Valves depressed at the centre, otherwise flat, with elevations sloping upwards towards the apices, *c*. 1 μm tall and *c*. 3 μm long, central portion elliptical tapering into narrow projections rounded at the apex, 65–125 μm long, 21–31 μm wide, the projections 3–4.5 μm wide. Mantle separated from the valve face by a sharp angle, sloping slightly outwards, 4–5 μm deep, with vertical striae 7–8 in 10 μm reaching almost to the margin. Central area subcircular, 10–13 μm in diameter. Areolae *c*. 0.3 μm in diameter, on the valve face in radial striae, striae 6–10 in 10 μm, areolae 4–6 in 10 μm, but striae and areolae closer close to the central area and near the apices. Periplekton with a circular stem 1.75–2.5 μm in diameter, *c*. 6 μm tall, close to that of the sibling valve, ring small, subcircular, 6–7.5 μm in diameter, closely clasping the stem of the sibling periplekton, arms unequal, the shorter arm extending for *c*. 180°, the longer for *c*. 300°, its tip deflected downwards; line joining the centres of the stems of sibling periplekta on the apical axis or inclined at up to 30° to it. Ocelli elliptical, *c*. 1.5 μm broad, 3 μm tall, transverse, inclined at 10°–15° to the vertical. Marginal spines extending to the apices, 4–5 in 10 μm, on the central portion of the valve

c. 6 μm tall, expanded above and interlocking, with small tubercles on the outer side near the base. No superficial spines.

Middle Eocene. Falkland Plateau, south-western Atlantic Ocean, 51° 08′S, 54° 22′W, 1525 m depth. Vema cruise 17, core 107, 50 cm (CAS 216030*), 120 cm (BM 78198; CAS 82033, 216027), 175 cm (CAS 216025).

Late Eocene. Oamaru, Otago, New Zealand (BM 33316 Jackson's Paddock, 60840 Williams' Bluff, 69161 (= Tempère & Peragallo, Diatom Monde ent. no. 810) Troublesome Gully, 77754 Jackson's Paddock, coll. Adams G639 Jackson's Paddock (holotype), coll. Morley Jones s.n. Jackson's Hill; PH coll. Shulze arr. 824).

There are many resemblances between *Rutilaria australis* and both *R. elliptica* Greville and *R. philippinarum* Cleve & Grove. Their periplekta are very alike; all three species having small rings without flanges on the unequal arms. Also the arrangement and spacing of the areolae on the valve face is very similar. *R. elliptica* and *R. philippinarum* both have the same wide range in outline, from specimens with elliptical valves to others with long subcapitate projections. All the specimens seen of *R. australis*, except one, have valves with an elliptical central portion that tapers into projections that themselves taper very gradually to the apices, which are never subcapitate. The one exception (CAS 216027) is an elliptical valve 80 μm long and 31 μm wide that is larger than the elliptical central portion of any of the others. The diameter of the ring of its periplekton is also unusually large. Somewhat similar anomalous specimens of *R. elliptica* have also been found (see pp. 47–48, above). *R. australis* resembles *R. elliptica* and differs from *R. philippinarum* in having marginal spines extending to the apices but no superficial spines, and also in having elevations at the apices. On the other hand, it resembles *R. philippinarum* and differs from *R. elliptica* in having vertical striae on the mantle. It is clearly a species distinct from both of these. In the past, however, I did not recognize this, but misidentified specimens from the Falkland Plateau as *R. philippinarum* (Ross, 1976). I also identified specimens from Oamaru in BM as *R. philippinarum*, and Desikachary & Sreelatha (1989) accepted these determinations when preparing their account of the diatoms from that fossil deposit.

Rutilaria australis has been found in a core from the Falkland Plateau which recovered middle Eocene material and also in the upper Eocene diatomite at Oamaru, New Zealand. Both these localities are in the southern hemisphere, hence the specific epithet.

24. **Rutilaria philippinarum** Cleve & Grove in *Diatomiste* **1**: 64, pl. 10 figs 1, 2 (1891). – Mann in *Bull. U. S. natn. Mus.* **100**(6): 143 (1925). – Desikachary & Sreelatha, *Oamaru Diatoms. Biblioth. Diatomol.* **19**: 225, pl. 96 figs 1, 7 (1989), excl. pl. 96 figs 2, 5, 6, 8. Figs 64–67, Plate XVII (a)–(f).

Rutilaria ventricosa sensu Pantocsek, *Beitr. foss. Bacill. Ung.* **1**: 44, Taf. 9 fig. 78 (1886); op. cit. **2**: 74 (1889), non Greville.
Rutilaria pulchra A. Schmidt, *Atlas Diatom.-Kunde*: Taf. 183

fig. 20 (1893). – Mann in *Bull. U. S. natn. Mus.* **100**(6): 143 (1925).
Rutilaria hexagona sensu Cleve in *K. svenska VetenskAkad. Handl.* (Ny Följd) **35**(5): 31 (1901), non Grunow.

Frustules up to 35 μm deep. Valves slightly or not at all depressed at the centre, without any elevations at the apices; valves 35–200 μm long, 16–32 μm wide, lanceolate with obtuse apices or with a central portion with moderately convex margins tapering gradually into projections with cuneate and, in the longer valves, capitate apices, the projections (2.5–)6–11 μm broad, apices (5–)7–17 μm broad. Mantle separated from the valve face by a sharp angle, sloping slightly outwards, 4–7 μm deep, with vertical striae reaching almost to the margin in the central part of the valve but shorter near the apices. Central area circular, *c.* 2/5 of the width of the valve in diameter. Areolae 0.3–0.5 μm in diameter, on the valve face in rather indistinct radial striae, striae 6–12 in 10 μm, areolae 4–8 in 10 μm near the central area, closer and sometimes decussate near the apices, especially in specimens with projections. Periplekton with a circular stem *c.* 2.5 μm in diameter, 6–10 μm tall, close to or touching that of the sibling valve; ring small, subcircular, 5–8.5 μm in diameter, closely clasping the stem of the sibling periplekton, the arms unequal, the shorter arm extending for 90°–180°, the longer arm for 270° or more, its tip bent towards the valve from which it arises; line joining the centres of the stems of sibling periplekta on the apical axis or inclined to it at up to 20°. Ocelli *c.* 3 μm × 5 μm, transverse, slightly inclined to the vertical, porelli 50–60 in 10 μm. Marginal spines 7–10 μm tall, expanded at the tip and interlocking with those of the sibling valve, with small tubercles on the outside at, or just above, their bases, not present near the apices and often absent throughout the projections, 3–6 in 10 μm, inserted *c.* 2 μm proximal to the outer edge of the valve face. Superficial spines present at the proximal end of the projections, or close to the apices in specimens without projections. Mature cingulum consisting of three copulae; valvocopula with a pars exterior 5–8 μm deep; copula II with a pars exterior 2–4 μm deep; copula III with a pars exterior 1–4 μm deep; valvocopula and copula II with vertical striae, striae and areolae *c.* 18 in 10 μm, and with a line of areolae *c.* 18 in 10 μm at the junction of the pars exterior and the pars interior; copula III with a double row of areolae *c.* 18 in 10 μm.

[**Early Eocene**. Sengilei, Ulyanovsk oblast, Russia (BM 36246).]

Late Eocene. Oamaru, New Zealand (BM 11096, 33317 Jackson's Paddock, 36124 Dick's Farm, 74145, 76834 Jackson's Paddock, 77754 Jackson's Paddock, 77758 Allan's Farm, 77760, 90987 Jackson's Paddock, 90990 Jackson's Paddock, coll. Adams J3856, coll. Morley Jones s.n. Papakaiyo, s.n.; G, coll. Brun 141N; US 7211 Jackson's Paddock).
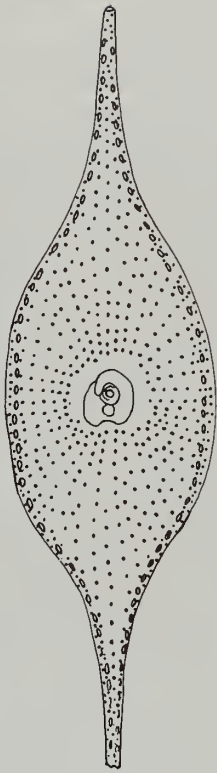
Early Miocene. St. Laurent-la-Vernède, Gard, France (BM SEM 36690–36692).

Middle Miocene. Pôtor (Szent Peter), Banská Bystrica region, Slovakia (BM coll. Adams W345; BRM H.t.48).
Velky Krtis (Nagykürtös), Banská Bystrica region, Slovakia (Pantocsek, 1889).
Nográdszakál (Szakal), Nograd & Hont County, Hungary (Pantocsek, 1886).

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* The diatom collection at CAS has been re-numbered since 1976, and this is the specimen figured as Ross, 1976: pl. 1 fig. 5.
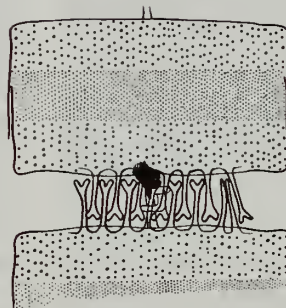
Figs 62–67   Figs 62–63: *Rutilaria australis*, valve view, × 1000, BM coll. Adams G639, Jackson's Paddock, Oamaru, New Zealand, holotype. Figs 64–67: *Rutilaria philippinarum*, × 1000. Fig. 64: valve view, BM 10534, Manila, Philippine Islands; Fig. 65: girdle view, BM coll. Adams G344, Makassar Strait, Indonesia, lectotype; Fig. 66: valve view, BM 10534, Manila, Philippine Islands; Fig. 67: valve view, BM 74145, Oamaru, New Zealand.

Late Miocene. Paradise Beach, Malibu, Los Angeles County, California, U.S.A. (BM SEM CB09.504–518, CB14.149–153, 36523–36530, 71393, 71394).

Malaga Cove, Los Angeles County, California, U.S.A. (Specimens labelled Redondo Beach, San Redondo and Santa Monica are included here, see Hanna 1928*b*, 1936). (BM 33239, 58814, 64665, 68393 (= Tempère & Peragallo, Diatom. Monde ent. no. 47); G coll. Brun 4322, 4323).

Maria Madre Island, Mexico (BM 78211, 78212, 78213).

Recent. Zanzibar, Tanzania (BM 3553).

Coast of Arabia (MANCH coll. Chaffers arab.75).

Bali Sound, Indonesia (Cleve, 1901).

Makassar Strait, Indonesia (BM coll. Adams G344 (lectotype), G356 (syntype), G382 (syntype), GC2667).

Philippine Islands (BM coll. Adams M58, M59, TS518; US 3161, 3162, 3163, 3164, 3165, 3166, 3168, 3169).

Jolo, Sulu Archipelago, Philippine Islands (US 3167).

Mindoro Strait, Philippine Islands (BM coll. Adams GC2712).

Manila, Philippine Islands (BM 10534).

The specimens of *Rutilaria philippinarum* from the Makassar Strait mounted by Grove are all part of the original material on which the protologue of the species was based and are therefore syntypes. G344 and G356 are both selected slides and the specimens on them are mounted in girdle view, as are two of the three specimens on G382, which is a strewn slide. Any one of these may have been the original of figure 1 in the protologue, which depicts a specimen in girdle view. A third specimen on G382 is in valve view, but it has a slight projection at one end and cannot be the original of fig. 2. As no holotype was designated by Cleve & Grove, I here designate the specimen in BM coll. Adams G344 as lectotype. Fig. 65 illustrates this specimen.

Rutilaria philippinarum is one of the species in which the apical axis has a very considerable range in length, the shorter specimens being lanceolate in outline (Cleve & Grove, 1891: pl. 10 fig. 2) whilst the longer ones have projections (Figs 64, 66, 67, Plate XVII (a)), the longest of which are capitate and cuneate. The projections are normally at least 6 μm broad at their narrowest part and expand somewhat towards the apices. One specimen from the upper Eocene of Oamaru (BM coll. Adams J3856), however, has very narrow projections, only 2.5 μm at their narrowest part, expanded to 5 μm close to the apices; another from the lower Miocene of St. Laurent-la-Vernède (BM SEM 36690–36692), France, has projections 4 μm wide, expanding to 6 μm. Many recent specimens, including those on which the original description is based, are short and have no projections, although in others projections of considerable length are present. On the other hand, almost all fossil specimens have projections, although on some (e.g. BM 11096 from Oamaru, New Zealand, and G coll. Brun 4323 from Malaga Cove ('Redondo Beach'), California, U.S.A.) they are quite short. The specimen from Malaga Cove ('Santa Monica'), California, U.S.A., on which Schmidt based *R. pulchra* has long subcapitate projections, and it is scarcely surprising that he failed to realize that it belonged to the same species as those figured by Cleve and Grove in their protologue of *R. philippinarum*. There is a specimen in BM consisting of a chain of frustules only 40 μm long and without projections that is labelled as coming from 'Singiliewsky', i.e. from Sengilei in the middle Volga basin, Russia, where an early Eocene, or

possibly Paleocene, deposit occurs. No other specimen of the species has been found in this deposit or in any other Paleocene or early Eocene material from the Volga basin or elsewhere. The specimen was mounted by S.H. Meakin, many of whose slides contain specimens that are obvious strays. The only other specimens with as short an apical axis that I have seen are all recent. It thus seems probable that this specimen did not, in fact, come from the locality indicated.

Rutilaria philippinarum and *R. australis* R. Ross are the only species of the genus to have areolae in vertical striae on the greater part of the mantle. In *R. areolata* and *R. schenkii* clusters of small, irregularly arranged areolae are present on the mantle close to each apex, the remainder of the mantle being hyaline. In all the other species of the genus the mantle is hyaline throughout.

The earliest description and figure of *Rutilaria philippinarum* was by Pantocsek (1886), who had found the species in the middle Miocene at Pôtor (Szent Peter), Slovakia and Nográdszakál (Szakal), Hungary. He identified it as *R. ventricosa* Greville, a synonym of *R. elliptica* Greville, a very similar, but nevertheless distinct, species. The differences between *R. philippinarum* and *R. elliptica* are discussed above (p. 48) under the latter species. The identity of the specimen illustrated by Pantocsek is obvious from his figure, and is confirmed by specimens of *R. philippinarum* from the outcrop at Pôtor (Szent Peter), Slovakia, that I have been able to examine.

Cleve (1901) records *Rutilaria hexagona* Grunow (a synonym of *R. obesa* Cleve) from a plankton sample taken in Bali Sound, Indonesia, but does not provide a figure. This record is almost certainly based on a misidentification, as *R. obesa* is known only as fossil from the late Oligocene to the middle Pliocene. The two living species of *Rutilaria* both occur in the seas around Indonesia, but only *R. philippinarum* might be misidentified as *R. hexagona*; *R. tenuicornis* Grunow is much too different in outline. Cleve's record is therefore accepted as being based on *R. philippinarum*. W.A. Firth made a similar mistake; a specimen of *R. philippinarum* from the Mindoro Strait, Philippine Islands, that he had mounted was labelled by him '*Rutilaria hexagona*'.

Only two of Desikachary & Sreelatha's (1989) six figures said to illustrate *Rutilaria philippinarum* actually show this species. Figures 2, 5 and 8 of plate 96 are of *R. australis* R. Ross, figures 5 and 8 being of the same specimen, and fig. 6 is of *R. areolata* R. Ross subsp. *areolata*.

The earliest certain occurrence of *Rutilaria philippinarum* is in the upper Eocene deposit at Oamaru, New Zealand. The species has persisted from the late Eocene until the present day, but it has been uncommon to rare in all the samples in which it has been found. It is interesting that its only occurrence in the Paleogene is in the southern hemisphere whilst its Neogene fossil occurrences are all in the northern hemisphere, although that may result from nothing more than the incompleteness of the fossil record. The incompleteness of that record is also shown by the fact that no specimens from the Pliocene or Pleistocene have been found, although it must have existed throughout those periods. At the present day it is apparently confined to inshore waters of the Indian Ocean and western Pacific, where it has been found both in plankton samples and in bottom muds. Those in the latter are presumably dead frustules that have settled out of the water column.

25. **Rutilaria attenuata** R. Ross, **sp. nov.**
Figs 68, 69.

Valvae ab centro ad apices uniformiter decrescentes, ad pices parum elevatae, 100–125 μm longae, 10 μm latae, ad apices 2.5 μm latae. Limbus ab fronte indistincte separatus, hyalinus, c. 1 μm altus. Area centralis circularis, diametro c. 6 μm. Areolae poroides, diametro 0.4–0.5 μm, in striis radiatis 12–16 in 10 μm dispositis, areolis prope centrum valvae 6–7 in 10 μm, prope apices creberrimis et 14–17 in 10 μm. Periplekton caule circulari diametro c. 1.2 μm, ad eum valvae fraternae approximato vel appresso, ad summum transtro siliceo c. 1 μm lato, ad unum marginem valvae extenso. Ocelli transversi, ab verticali c. 20° inclinati, diametro c. 1.5 μm. Spinae marginales acutae, 4–6.5 in 10 μm, ab margine frontis c. 1.5 μm distantes, ad apices attingentes, sine tuberculo ad basim, eae plus distales plerumque centrales et extensionibus basalibus longitudinalibus costatis instructae, extensione juxta elevationem terminalem ad eam conjunctam. Spinae superficiales nullae.

TYPUS. In BM 52749 in stratis eocaenicis superioribus ad 'Oamaru, Otago', Novam Zelandiam

Valves 100–125 μm long, 10 μm broad, tapering uniformly from the centre to the apices, which are 2–2.5 μm broad and probably slightly raised. Mantle not sharply separated from the valve face, c. 1 μm deep, hyaline. Central area circular, c. 6 μm in diameter. Areolae 0.4–0.5 μm in diameter, in radial striae 12–16 in 10 μm, the areolae 6–7 in 10 μm close to the centre of the valve but much closer, 14–17 in 10 μm, near the apices. Periplekton with a circular stem c. 1.2 μm in diameter, very close to or touching that of the sibling valve, and at its tip a transverse bar of silica c. 1 μm wide extending to the margin on one side of the valve; line joining the centres of the stems of sibling periplekta on the apical axis. Ocelli c. 1.5 μm in diameter, transverse, inclined at c. 20° to the vertical. Marginal spines pointed, without any tubercle at the base, reaching to the apices, 4–6.5 in 10 μm, inset c. 1.5 μm from the margin of the valve, the most distal marginal spines usually central and with longitudinal costate extensions at their base, that nearest the terminal elevation fused to it. No superficial spines.

Late Eocene. Oamaru, Otago, New Zealand (BM 52749 (holotype); coll. Woodward s.n.).

This is an extremely rare species of which only two specimens are known. The holotype consists of a sibling pair of valves united by their periplekta; the other specimen is a single valve with the stem of the periplekton broken across. As both specimens are mounted in valve view, no information is available about the girdle or the height of the periplekton and the marginal spines. Slight terminal elevations appear to be present, but there cannot be complete certainty about this.

Only one specimen of *Rutilaria attenuata* has a periplekton that is apparently intact and this is abnormal, in the sense that its structure differs from that normally found in *Rutilaria*. There seems to be no ring at the top of the stem but only a transverse bar of silica. This may, however, not be the entire periplekton; part may have broken away.

The affinities of *Rutilaria attenuata* are very uncertain. In the arrangement of its areolae it is closer to *R. elliptica* Greville, *R. australis* R. Ross and *R. philippinarum* Cleve & Grove than to any other species, but the marginal spines are without tubercles at their bases and the most distal ones have longitudinal costate extensions. In these characters it resembles *R. tenuicornis* Grunow and *R. briggeri* R. Ross and

its outline is close to that of the latter species. Another species with the same outline as *R. australis* is *R. lanceolata* Grove & Sturt and this also has the mantle not sharply separated from the valve face, an unusual character in the genus. There are thus some indications that *R. australis* may be related to the group of species that includes *R. elliptica* and others that suggest that it is related to the group that includes *R. briggeri* and *R. lanceolata*. When more specimens have become available, it will become apparent whether the periplekton of the holotype is normal for the species and, if it is not, whether *R. attenuata* has a periplekton which resembles that of *R. elliptica* or that of *R. briggeri*.

This species is much narrower in proportion to its width than most species of *Rutilaria*, and the specific epithet was chosen for this reason. Both the specimens of this species were originally identified as *R. lanceolata* Grove & Sturt, a species with a very similar outline that also occurs in the upper Eocene deposit at Oamaru, New Zealand. That species, however, has much finer areolation and is completely lacking in marginal spines.

26. **Rutilaria szakalensis** Pantocsek, *Beitr. foss. Bacill. Ung.* **2**: 74, Taf. 24 fig. 355 (1889). – De Toni, *Syll. alg.* **2**: 1023 (1894).
Figs 70, 71, Plate XVIII (a)–(f).

Rutilaria sp. Chenevière in *Földt. Közl.* **63**: 217 (1933); *Bull. Soc. fr. Microsc.* **3**: 36 (1934).

Mature frustules c. 40 μm deep. Valves flat, with apical elevations rounded above, c. 3 μm tall, c. 6 μm long, rising abruptly from the valve face; valves 53–127 μm long, 25–57 μm wide, broadly lanceolate. Mantle separated from the valve face by a sharp angle or slight marginal ridge, vertical, 5–7 μm deep, hyaline. Central area circular, 7–13 μm in diameter. Areolae c. 0.2 μm in diameter, in radial striae, striae 6–8 in 10 μm, areolae 4–7 in 10 μm. Periplekton with a circular stem c. 3 μm in diameter, c. 9 μm tall, appressed to that of the sibling valve; ring circular, 7–8 μm in diameter, closely clasping the stem of the sibling periplekton, the arms unequal, the shorter extending for c. 150°, the longer for c. 360°, its tip bent towards the valve from which it arises; line joining the centres of the stems of sibling periplekta at 5°–45° to the apical axis. Ocelli 2–2.5 μm in diameter, transverse, vertical to inclined at 30°, porelli c. 50 in 10 μm. Marginal spines extending to the apices, 3–4 in 10 μm, inserted c. 2 μm proximal to the outer edge of the valve face, 8–9 μm tall, expanded at the tip and interlocking with those of the sibling valve except for a few pointed ones close to the apices, very small tubercles c. 2.5 μm above the valve face on the outside of all marginal spines except those close to the apices. Blunt, conical superficial spines scattered over the valve face, from very many 3–5 μm apart to only two to three, occasionally none. Mature cingulum consisting of three copulae; valvocopula an open band, hyaline, with a pars interior 3.5 μm deep and a pars exterior 8 μm deep, with an abvalvar indentation at the closed apex; copula II an open band with a large ligula at the apex where the valvocopula is open, the pars exterior c. 6 μm deep with two rows of areolae 22 in 10 μm along its advalvar edge; copula III an open hyaline band with a large ligula, the pars exterior c. 2 μm deep.

Early Miocene (for this date see below). Conset, Barbados (BM 78218).
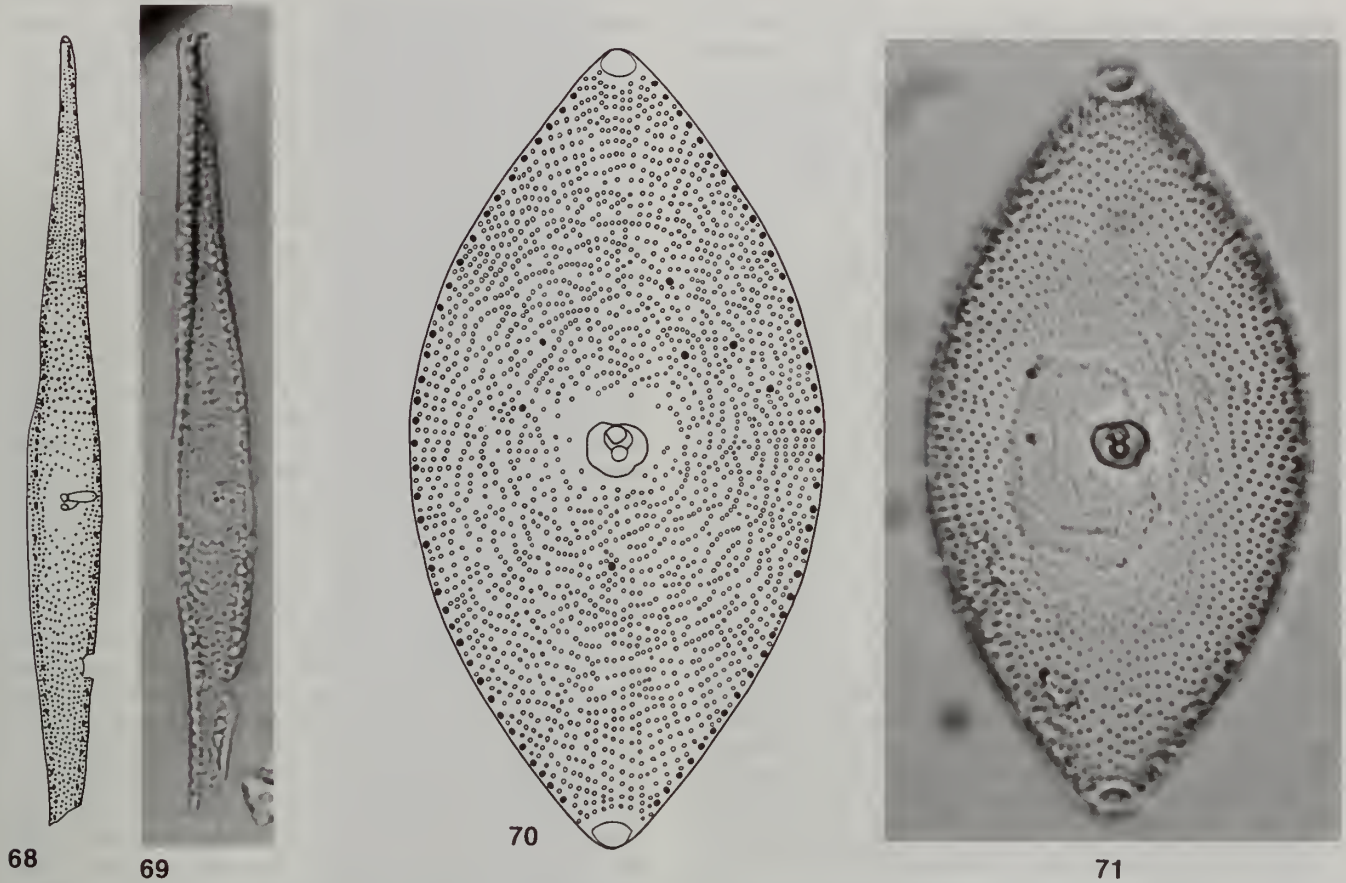
Figs 68–71 Figs 68–69: *Rutilaria attenuata*, valve view, × 1000, BM 52749, Oamaru, New Zealand, holotype. Figs 70–71: *Rutilaria szakalensis*, valve view, × 1000, BM coll. Adams G515, Pôtor, Slovakia, different specimens on same selected slide.

Middle Miocene. Pôtor (Szent Péter), Banska Bystrica region, Slovakia (BM 32865, 32866, 32868, 32869, 70426, 70427, coll. Adams G514, G515, G516; G, coll. Brun 4227).

Velky Krtis (Nagykürtös), Banska Bystrica region, Slovakia (Pantocsek, 1889).

Nográdszakál (Szakal), Nograd & Hont County, Hungary (Pantocsek, 1889).

'Castel', Szurdokpüspöki, Hungary (BM 64662, coll. Adams H858, TS719, TS738, coll. Morley Jones s.n., s.n., SEM B16.907, B16.909, CB14.045–062, CB14.260–271, CB15.678–681, 70399–70414; BRM H.t.45; CAS 65080, 67043, 67045). (The age of these specimens is uncertain; see p. 4).

Szurdokpüspöki, Hungary (CAS 67044).

There is now no specimen of *Rutilaria szakalensis* in the Pantocsek collection at BP, but it is obvious from his illustration that the specimens from Pôtor that I have seen belong to the same species as those he found in the deposits at Nogradszakal and Velky Krtis.

The periplekton of *Rutilaria szakalensis* (Plate XVIII (b)) is very similar to that of *R. barbadensis* R. Ross, *R. elliptica* Greville, *R. australis* R. Ross, and *R. philippinarum* Cleve & Grove, and the arrangement of its areolae (Figs 70, 71, Plate XVIII (a)) is also similar to that found in those species, although there are slight differences. *R. barbadensis* has closer areolae than any of the others. Also, the striae of *R. szakalensis* are more obviously radial than those of *R. elliptica*, *R. australis* and *R. philippinarum*; this is partly, perhaps,

because of its broader valves and partly because the areolae in the proximal part, at least, of the striae directed towards the apices are no more widely spaced than the striae themselves, whereas in the other three species they are much more distant than the striae. In *R. szakalensis*, however, the outline of the valve is very distinct (Figs 70, 71, Plate XVIII (a)); it never has projections and the apices are more acute than in those specimens of *R. philippinarum* and *R. elliptica* that are without projections. Also, the shape of its elevations, which rise abruptly from the valve face (Plate XVIII (f)), is different from that of the more gradually rising elevations of *R. elliptica* and *R. australis*.

Rutilaria szakalensis is infrequent but not rare in the middle to upper Miocene Tethyan deposits of Hungary and Slovakia. Chenevière (1933, 1934a) recorded *Rutilaria* sp. in the material from near Szurdokpüspöki, Hungary, that he later distributed with the locality given as 'Castel'; the presence of *R. szakalensis* in this material shows that this species is the one that he found there. A single specimen has also been found in material from Conset, Barbados. This is the only specimen seen that has no superficial spines, but as these vary so much in number on the specimens from central Europe, from more than 100 to only two, there is no reason for considering that it is taxonomically distinct. There are no other differences. As this species is known elsewhere only from Miocene deposits, the specimen from Conset presumably came from one of the lower Miocene samples from that locality rather than from one of middle Eocene or early
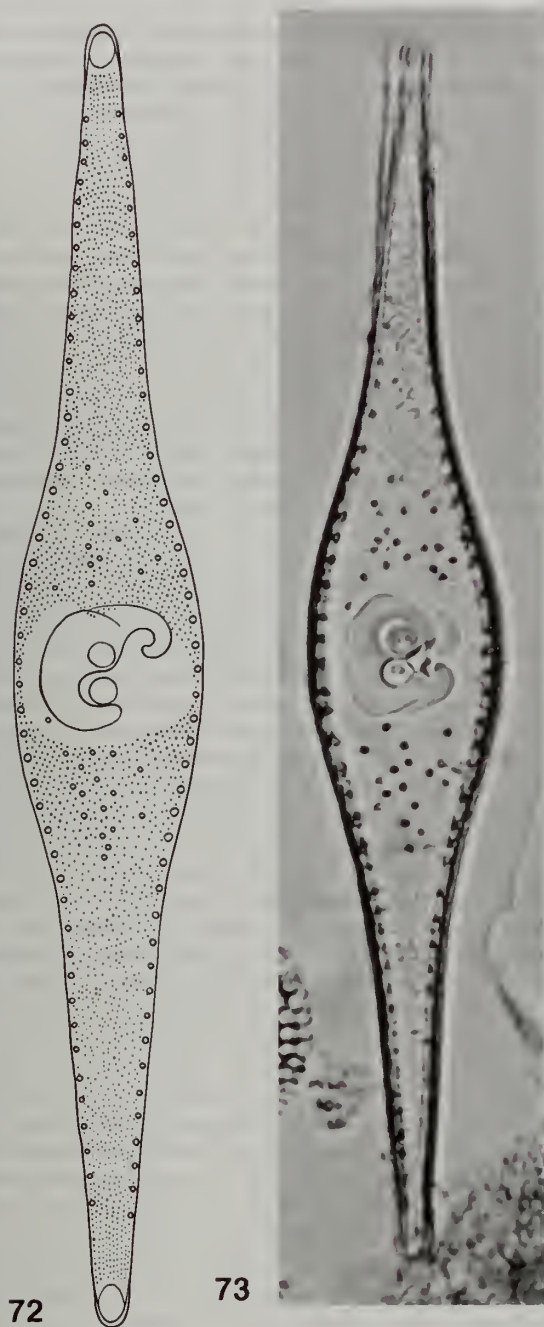
Figs 72–73 *Rutilaria epsilon*, valve view, × 1000, Monterey, Monterey County, California, U.S.A. Fig. 72: BM 58812; Fig. 73: BM 3376, neotype.

Aomori Prefecture, Honshu, Japan (Kanaya, 1959).

Abashiri, Hokkaido, Japan (BM 13639, 14870 (= Tempère & Peragallo, Diatomées no. 616), 14871 (= Tempère & Peragallo, Diatomées no. 617), 31645, 31646, 31647, 33327, 41666, 41667, 68797 (= Tempère & Peragallo, Diatom. Monde ent., no. 448), 68798 (= Tempère & Peragallo, Diatom. Monde ent., no. 449), coll. Adams B425, L3, TS97, SEM 96957–96959).

From an exposure near the mouth of the Kuybysheva river valley, on the right bank, Iturup island, Kuril islands, Russia (Kozyrenko & Sheshukova-Poretskaya, 1967).

Newport Beach, Orange County, California, U.S.A. (BM coll. Morley Jones s.n.; CAS 100021, 100022; MANCH coll. Chaffers N'port 39).

Middle Miocene–late Miocene. 'Santa Lucia, California', presumably from an outcrop on the eastern side of the Santa Lucia mountains, Monterey County, California, U.S.A. (BM 69194 (= Tempère & Peragallo, Diatom. Monde ent., no. 843)).

Middle Miocene–early Pliocene. California, U.S.A. (BM 78311, coll. Adams G544, SEM B4.394–411, 72740–72743).

Late Miocene. Sendai, Miyagi Prefecture, Honshu, Japan (BM 8145, 8146, 9283 (syntype of *R. longicornis?*), 9284, 15470, 31297, 31300, 31387, 31573, 31575, 31577, 31578, 31579, 31581, 32858, 32859, 32860, 32861, 32863, 33256, 33257, 34296, 41664, 41665, 41671, 52888, 52891 (syntype of *R. longicornis?*), 52903, 52905, 60833, 60834, 60835, 68370 (= Tempère & Peragallo, Diatom. Monde ent., no. 24), 70936, 70940, 70948, 70952, 74134, 74136, 74148, 76339, 76340, 78220, 78221, 78222, coll. Adams Bess. 506, C497, F1093, G317, G318, G322, GC2708, GC2713, GC2714, H213 (syntype of *R. longicornis?*), J566, J2840, J2841, J2842, TS267, TS268, TS463, coll. Morley Jones s.n., s.n., SEM 66197–66206, 72744, 72821–72823, 73081–73082, 73341–73348; BRM H.t.15, H.t.16, H.t.17, H.t.18, H.t.19, H.t.20, H.t.21, Zt.1.28; G coll. Brun 2816 (syntype of *R. longicornis*), 2816bis (syntype of *R. longicornis*); MANCH coll. Chaffers Send.F, s.n.: PC coll. Lefébure s.n., coll. Le Tourneur s.n.; PH Gen. coll. 35041, 35270, Coll. Boyer R-1-8; US 6094, 6095, 6097).

Wakura, Noto Peninsula, Toyama Prefecture, Honshu, Japan (Ichikawa, 1960).

Tokoro, Abashiri, Hokkaido, Japan (BM 14781 (= Tempère & Peragallo, Diatomées no. 527), 54891, 68436 (= Tempère & Peragallo, Diatom. Monde ent., no. 90), coll. Adams J4829, J4830).

Monterey, Monterey County, California, U.S.A. (BM 3376 (neotype), 7338, 11021, 32871, 32873, 45878, 49317, 49320, 58812, 58813, 67262, 70419, 70422, coll. Morley Jones s.n.; CAS 202065 (original of Hanna, 1928a: pl. 8 fig. 3)).

Lompoc, Santa Barbara County, California. U.S.A. (Barron, 1975).

Malibu, Los Angeles County, California, U.S.A. (BM SEM 97815–97820).

Malaga Cove, Los Angeles County, California, U.S.A. (Specimens labelled Redondo Beach, San Redondo and Santa Monica are included here, see Hanna, 1928b, 1936) (BM 7984, 11116, 31296, 32768, 32772, 32773, 32822, 33238, 33239, 33240, 33241, 33247, 33252, 45957, 54315, 54317, 60832, 64665, 64747, 66582, 70421, 70957, 70965, 70972, 70973, 71006, 91036, coll. Adams C494, F1090, F1091, H215, J1252, TS1, coll. Bastow 853; G coll. Brun 4322; MANCH coll. Chaffers RB130; PC coll. Lefébure s.n., coll. Le Tourneur s.n., coll. M. Vincent A 35; PH Gen. Coll. 8398, Coll. Boyer R-1-9, Coll. Shulze, arr. 1770; US 6003).

Channel Road, San Pedro, Los Angeles County, California, U.S.A (CAS 101049).

San Pedro, Los Angeles County, California, U.S.A. (BM 55072, 64669, 90965, coll. Adams G266; BRM H.t.22).

Los Angeles, Los Angeles County, California, U.S.A. (BM coll. Morley Jones s.n.).

River Ketovaya, Sakhalin, Russia (Sheshukova-Poretskaya, 1967).

From the foot of a 25 m high terrace escarpment on the

Okhotsk Sea coast, 1 km north-east of the village of Rybaki, Iturup Island, Kuril islands, Russia (Kozyrenko & Sheshukova-Poretskaya, 1967).

Late Miocene–early Pliocene. Ajigasawa, Aomori Prefecture, Honshu, Japan. (BM 78219, SEM CB19.879–881).

Sado-shima, Japan (PC coll. Le Tourneur s.n.).

Oyanabezawa, Aomori City, Aomori Prefecture, Honshu, Japan (Tsumura, 1964).

Setana, Hiyama, Hokkaido, Japan (BM 76061, 76338, coll. Morley Jones s.n., s.n., s.n.).

Kabaoka, Wakkanai, Rumoi, Hokkaido, Japan (Tsumura, 1964).

Embetsu, Rumoi, Hokkaido, Japan (BM 69101 (= Tempère & Peragallo, Diatom. Monde ent., no. 750 as 'Wembets')).

Teshio, Rumoi, Hokkaido, Japan (Pantocsek, 1892, 1905 as 'Thesiogori' or 'Theshiogori').

Santa Maria, Santa Barbara County, California, U.S.A. (BM 14372 (= Tempère & Peragallo, Diatomées no. 120), 54318, 70420, coll. Adams GC2710; G coll. Brun 1236; PC coll. Le Tourneur s.n.).

Late Miocene to early Pliocene. Basin of the river Savan, Kamchatka, Russia. (Sheshukova-Poretskaya, 1967).

[**Recent**. 'Chinese canned fish.' (BM coll. Morley Jones s.n.).]

Rutilaria epsilon was first found by Kitton in a sample from the upper Miocene of Monterey, California, U.S.A. He mistook the valve view of the species for the girdle view and interpreted the marginal spines as the keel puncta (fibulae) of a *Nitzschia*. He sent both a description of the species and a specimen to Greville using that generic name. Greville recognized that it belonged to a distinct genus which also included two species (actually only one, *R. elliptica* Greville) that he found in material from Cambridge, Barbados; for this genus he published the name *Rutilaria* (Greville, 1863). He accepted Kitton's view that the actual valve view was a girdle view, although expressing some doubt, saying: 'I have formed the generic character on the assumption that this little group [*R. epsilon, R. elliptica, R. ventricosa*] belongs, with *Nitzschia*, to the *Fragilarieae*, and that the figures consequently represent a front view. But it must be confessed that, for a front view, the appearance is a little strange.' He later (Greville, 1866) realized his mistake.

On Greville's original drawing of his published figure of *Rutilaria epsilon* there is no indication of the slide on which it is based and this cannot be traced either in his collection or in the part of Kitton's collection that is preserved in BM. A specimen in Greville's collection that came from the type locality (Fig. 73) was accordingly designated as neotype by Williams (1988).

Brun did not indicate in the manuscript catalogue to his collection whether any one of the specimens in it should be regarded as the holotype of *Rutilaria longicornis* Brun & Tempère. One does not know whether the original of the figure that accompanied the publication of the name remained in his hands or in Tempère's, although one of the eleven specimens on his slide no. 2816 from Sendai matches the figure very closely. All of the specimens that he identified as *R. longicornis*, i.e. those on slide 2815bis from 'Yedo' (= Tokyo-wan) and slides 2816 and 2816bis from Sendai, must be regarded as syntypes. The status of specimens from either locality mounted by Tempère is more doubtful; many of them

were no doubt prepared at a later date but they should presumably be regarded as at least isosyntypes. Such slides include BM 9283, BM 52891 and BM coll. Adams H213.

The specific epithet of *Rutilaria epsilon* was given to the species because the superimposed periplekta of two sibling valves as seen under the light microscope have an appearance that resembles that Greek letter. The shorter arm of the ring does not even partially encircle the stem of the sibling periplekton; instead it forms a hook that clasps the tip of a branch arising near the distal end of the longer arm of the sibling periplekton, and this gives the appearance of the Greek letter *epsilon* (Fig. 73, Plate XIX (b), (c)). This character readily distinguishes the species from all others in the genus. The girdle of *R. epsilon* is also distinctive. Although the valvocopula is an open band, copula II has no ligula. The valvocopula narrows gradually towards its open end and copula II slopes towards this apex of the valve without becoming broader (Plate XIX (e)).

In spite of the very distinctive periplekton of *Rutilaria epsilon*, and the clarity with which Greville's (1863) original figure shows it, the limits of the species, and even its true identity, have been much misunderstood in the past. There has been a strong tendency to associate with it as a variety any member of the genus with a long narrow outline, or with areolae not arranged in regular radiating striae. Grunow (in Van Heurck, 1883) thought it possible that both *R. hexagona* Grunow (= *R. obesa* Greville ex Cleve) and *R. tenuicornis* Grunow should be regarded as varieties of *R. epsilon*. Grove & Sturt (1887a) described *R. tenuis* Grove & Sturt as a variety of *R. epsilon*, although they called it a new species in the legend to their illustration of it. Brun & Tempère (1889) suggested that *R. capitata* Brun & Tempère (= *R. obesa*) might also be a variety of *R. epsilon*. They made the same suggestion about *R. longicornis* Brun & Tempère, another species that they described from Sendai, Japan, that is an undoubted synonym of *R. epsilon*. *R. obesa*, *R. tenuicornis* and *R. tenuis* are, however, species quite distinct from *R. epsilon*.

The reasons given by Brun & Tempère (1889) for separating *R. longicornis* from *R. epsilon* were: 'La *R. Epsilon* Grev. (M.J.9.*1*) est dessinée avec des perles medianes rondes et un grand espace lisse autour du cône centrale.' Greville's original figure of *R. epsilon* (1863: pl.9 fig. 1) shows fine areolae over the whole surface, except for a central area scarcely larger than the ring of the periplekton, and it also shows the superficial spines, called by him 'large scattered puncta' and by Brun and Tempère 'perles rondes'. Examination of a long series of specimens from both California and Japan shows that there is no basis for any taxonomic separation. Individuals differ only in size and in the outline of their projections. Japanese specimens have a greater range of size, 73–450 μm × 22–37 μm, than those from California, which are 127–310 μm × 22–31 μm. The longer Japanese specimens, those 250 μm or more in length, have projections with parallel sides and some of these have subcapitate apices up to 15 μm wide, whilst the smaller Japanese specimens have tapering projections narrowed at the apices, which are 2.5–6 μm broad. Only one of the Californian specimens seen, CAS 100022 from Newport Beach, is long enough to have projections with parallel sides; the others, all 250 μm or less in length, have tapering projections. There is no detectable difference between the Californian and Japanese specimens of the same length, and there is equally no doubt that all the Japanese ones are part of the same population.

Four specimens of *Rutilaria epsilon* are illustrated in photomicrographs of diatoms from the Oligocene of the Komandorsky Islands sent me by Dr A.Yu. Gladenkov of the Institute of the Lithosphere, Moscow. One of these is smaller than any other specimen that I have seen, being only 50 μm × 20 μm, and two of the others, although much longer, about 120 μm, are no wider. Gladenkov (1991) includes *R. epsilon* in the list of early Oligocene species from this locality.

Tempère and Peragallo included slides from Tokoro, Japan, in both the published sets that they issued and listed *Rutilaria capitata*, but no other species of the genus, in the list of species present (Tempère & Peragallo, 1893, 1908). There are specimens of *R. epsilon* but none of *R. obesa*, of which *R. capitata* is a synonym, on the slides from this locality in the examples of these sets in BM. There are also in BM other specimens of *R. epsilon*, but none of *R. obesa*, from Tokoro. It must be assumed, therefore, that the inclusion of *R. capitata* in the lists of species from there is the result of misidentification.

Mann (1907) took an extremely broad view of the circumscription of *Rutilaria epsilon*, which he recorded from Albatross Station 4029H in the Bering Sea. This is the only species that he recorded from that locality, and he listed as synonyms *R. tenuicornis* Grunow, *R. longicornis* Brun & Tempère, *R. hexagona* Grunow, *R. szakalensis* Pantocsek, *R. kerneri* Pantocsek, *R. capitata* Brun & Tempère, *R. radiata* Grove & Sturt, *R. edentula* Castracane, *R. obesa* Greville ex Cleve, *R. superba* Greville, *R. elliptica* Greville, and *R. ventricosa* Greville, with the following comment: 'This species is subject to great variation. A good gathering will show all the forms represented by the above names, together with intergradations.' From this it is clear that he considered the outline of the valve as the only character that might, but did not, distinguish species and ignored all the other features of the specimens. *R. epsilon*, *R. hannai* subsp. *diomedeae* R. Ross and *R. obesa* all occur in the material recovered from Albatross Station 4029H.

More recently Jousé (1955) misapplied the name *Rutilaria longicornis*, a synonym of *R. epsilon*, to another species, *R. kamyshlovensis* R. Ross, which dates from the early Eocene. Sheshukova-Poretskaya (1967) accepted this identification by Jousé when reporting *R. epsilon* var. *longicornis* (Brun & Tempère) A. Schmidt from the Neogene of Sakhalin and Kamchatka, although her illustration shows that her identification was correct. She accordingly attributed to the species a fossil record from the late Eocene to the Pliocene, whereas its actual first appearance was not until the early Oligocene. The possibility that other Russian authors may have followed Jousé's identification means that any records unaccompanied by illustrations must be regarded as uncertain and they are therefore not listed here, except for the record by Kozyrenko & Sheshukova-Poretskaya (1967) from Iturup Island; there is no reason for doubting that the name is used by them in the same sense as it is by Sheshukova-Poretskaya (1967: 235, tabl. 41 fig. 2). Nevertheless, in the following year Glezer & Sheshukova-Poretskaya (1968) misidentified as *R. epsilon* var. *longicornis* specimens of *R. tenuicornis* subsp. *paleogena* R. Ross from the upper Eocene of the Ukraine.

One specimen from Japan, BM 15470, which is 402 μm long, seems to be an initial valve. Its projections are 16 μm wide and do not taper, its areolae are irregularly distributed throughout, not in longitudinal striae on the distal part of the projections, its superficial spines are much more numerous than usual and extend almost to the apices, and its periplek-

ton is vestigial. However, an even longer specimen, BM 52888, which is 450 μm long, has none of these unusual characters.

There are many resemblances between *Rutilaria epsilon* and *R. obesa* Greville ex Cleve that are discussed below (p. 62) under that species. *R. epsilon* also resembles *R. hustedtii* R. Ross, *R. barbadensis* R. Ross, *R. elliptica* Greville, *R. australis* R. Ross, *R. philippinarum* Cleve & Grove and *R. szakalensis* Pantocsek in having tubercles on the outer side of the proximal marginal spines. In *R. epsilon* the marginal spines are laterally expanded above, but they only abut (Plate XIX (f)) and do not interlock as in most of those species. *R. epsilon*, like them, has a periplekton with very unequal arms to its ring, but this is much larger, its shorter arm is of a different shape, and there is a poorly defined flange on the longer arm which can be seen on scanning electron micrographs but not under the light microscope (Plate XIX (a)–(c)). Two other species have tubercles on the marginal spines. One of these is *R. areolata* Sheshukova-Poretskaya, which also resembles *R. epsilon* in having protrusions along the upper margin of the ocellus (compare Plate XIX (d) with Plate VII (d), (f)). In all other respects, however, and especially in the presence of the winged costa on *R. areolata*, the two species are very different. The other species with tubercles on the marginal spines is *R. kamyshlovensis* R. Ross, but this has scarcely any other point of resemblance to *R. epsilon*.

The earliest records of *Rutilaria epsilon* are from the early Oligocene of the Komandorsky Islands and from the late Oligocene of the Navarin Basin in the Bering Sea. The age of some of the many deposits from California and Japan in which the species occurs is not known precisely, but they are certainly Miocene or early Pliocene. None of the records from these two areas that are dated more closely are from the early Miocene and there is no evidence of the occurrence of the species there earlier than the middle Miocene, although it is recorded from the early Miocene of the Aleutian Basin in the Bering Sea. There is also a record, not accompanied by an illustration and therefore not cited in the distribution given above, of *R. epsilon* from a dredge sample taken off Cape Arago, Oregon, U.S.A. and dating from the Miocene to Pliocene boundary (Whiting & Schrader, 1985); there is no reason to doubt the accuracy of the identification. The fossil record thus indicates that *R. epsilon* was, throughout its period of existence, confined to the northern part of the Pacific Ocean, from California and Japan northwards to the Bering Sea.

That statement about the distribution of *Rutilaria epsilon* is made on the assumption that three specimens of the species said to come from the late Eocene deposit at Oamaru, New Zealand, were not from that locality. One of these is on a slide of selected specimens from there mounted by Grove, and is presumably the basis of the record of the species from Oamaru by Grove & Sturt (1887a). It is not impossible, however, that this specimen is a contaminant as Grove also mounted specimens of *R. epsilon* from Californian and Japanese deposits. This is made probable by the fact that there can justifiably be doubts about the provenance of the only other specimens, two in number, that are said to come from this much studied deposit. CAS 355048 is a specimen sold by Messrs W. Watson & Sons and labelled as from Oamaru by a member of their staff. There are manifest errors in the labels of other microscope slides sold by this firm (see p. 24 sub *Rutilaria radiata*). There is also a specimen labelled as coming

from Oamaru and mounted by S.H. Meakin in the private collection of Mr Woodward. Many slides prepared by Meakin contain obvious contaminants and the evidence that the species actually occurs in the Oamaru deposit is thus very slight indeed.

There is another very dubious record based on a specimen mounted by A. Morley Jones and labelled 'Chinese canned fish'. This material, which was distributed by F.W. Adams, was obtained from the fluid in a can of fish imported into Britain from China; it consisted of recent marine species (see Fuge, 1937). The specimen of *R. epsilon* said to come from this is almost certainly a contaminant.

28. **Rutilaria obesa** Greville ex Cleve in *K. svenska Vetensk-Akad. Handl.* Ny Földj, **18**(5): 19 (1881) '*obesum*'. – De Toni, *Syll. alg.* **2**: 1022 (1894). – Williams in *Bull. Br. Mus. nat. Hist.* (Bot.) **18**: 46, pl. 53 figs 8,9 (1988). Figs 74–76, Plate XX (a)–(f).

Rutilaria hexagona Grunow in Van Heurck, *Syn. diatom. Belgique*: pl. 105 fig. 8 (1883). – Wolle, *Diatom. N. Amer.*: pl. 68 fig. 2 (1890). – J.D.Möller, *Diatom.-Präp.*: Taf. 6 Reihe 6 no. 3–4, Taf. 22 Reihe 8 no. 10–12, Taf. 23 Reihe 4 no. 28–29 (1891); *Verz. Lichtdrucktaf. Möll. Diatom.-Präp.*: 44, 145, 150 (1892). – A. Schmidt, *Atlas Diatom.-Kunde.*: Taf. 183 fig. 17 (1893). – Laporte & Lefébure, *Diatom. rares cur.* **2**: pl. 22 fig. 154 (1930). – Tsumura in *Bull. Yokohama City Univ. Soc.* **16**, Nat. Sci. 1: 87, pl. 2 fig. 2 (1964). – Barron in *Palaeontographica* **151**, B: 154, pl. 12 fig. 9 (1975).

Rutilaria capitata Brun & Tempère in *Mém. Soc. Phys. Hist. nat. Genève* **30**(9): 54, pl. 1 fig. 3 (1889). – J.D. Möller, *Diatom.-Präp.*: Taf. 23 Reihe 4 no. 24–25 (1891); *Verz. Lichtdrucktaf. Möll. Diatom.-Präp.*: 150 (1892). – Pantocsek, *Beitr. foss. Bacill. Ung.* **3**: Taf. 33 fig. 472 (1892); *Beschr. neu. Bacill.*: 94 (1905). – De Toni, *Syll. alg.* **2**: 1022 (1894). – Kanaya in Matsumoto (Ed.), *Palaeont. Soc. Japan, Twenty-Fifth Anniv. Vol.*: 23, pl. 35 fig.3 (1963). – Ichikawa, Fuji & Bachmann in *Sci. Rep. Kanazawa Univ.* **9**: 55, pl. 7 fig. 56 (1964).

Rutilaria hexagona var. *cornuta* Brun & Tempère in *Mém. Soc. Phys. Hist. nat. Genève* **30**(9): 55, pl. 1 fig. 2 (1889). – J.D. Möller, *Diatom.-Präp.*: Taf. 23 Reihe 4 no. 26 (1891); *Verz. Lichtdrucktaf. Möll. Diatom.-Präp.*: 150 (1892). – A. Schmidt, *Atlas Diatom.-Kunde*: Taf. 183 fig. 18, 19 (1893). – Kanaya in Matsumoto (Ed.), *Palaeont. Soc. Japan, Twenty-Fifth Anniv. Vol.*: 23, pl. 35 fig. 2 (1963). – Ichikawa, Fuji & Bachmann in *Sci. Rep. Kanazawa Univ.* **9**: 55, pl. 7 fig. 57 (1964). – Sheshukova-Poretskaya, *Neogen. Morsk. Diatom. Vodor. Sakhalina i Kamchatki*: 235, tabl. 41 fig. 3 (1967).

Rutilaria kerneri Pantocsek, *Beitr. foss. Bacill. Ung.* **3**: Taf. 33 fig. 474 (1892) '*kernerii*'; *Beschr. neuer Bacill.*: 94 (1905). – Jousé in Proshkina-Lavrenko et al., *Diatom. Analiz* **2**: 216, tabl. 100 fig. 6 (1949). – Tsumura in *Bull. Yokohama City Univ. Soc.* **16**, Nat. Sci. 1: 84, pl. 2 fig. 1 (1964) '*kinkeri*'. – Tsumura in *J. Yokohama City Univ.* **168**: 19, pl. 5 fig. 12 (1967) '*kinkerii*'. – Baldauf & Barron in *Bull. U. S. Geol. Surv.* **1765**: 3, 8, pl. 10 fig. 13 (1987).

Rutilaria cornuta (Brun & Tempère) Grunow ex Brun in *Diatomiste* **2**: 53 (1893).

Rutilaria epsilon var. *hexagona* (Grunow) De Toni, *Syll. alg.* **2**: 1021 (1894).

Rutilaria epsilon var. *cornuta* (Brun & Tempère) De Toni, *Syll. alg.* **2**: 1021 (1894).

Rutilaria elliptica sensu Laporte & Lefébure, *Diat. rares cur.* **2**: pl. 23 fig. 159 (1930), non Greville. – Tsumura in *Bull. Yokohama City Univ. Soc.* **16**, Nat. Sci. 1: 88, pl. 2 fig. 3 (1964).

Rutilaria sp. Hustedt, *Kieselalgen*: 54, Taf. 2 fig. 23–24 (1956).

Frustules 15–38 μm deep. Valves depressed at the centre, sloping down close to the margin, elsewhere flat, with apical elevations sloping up to flat tops, 1–2 μm tall, 4–6 μm long; valves 45–310 μm long, 30–73 μm broad, subhexagonal to broadly lanceolate with obtuse apices, or with a central portion with parallel to convex margins and with projections usually 7–18 μm broad and, except for the shortest, with subcapitate or capitate apices 10–30 μm broad; some of the broadest valves with short projections *c.* 30 μm broad at their base and tapering throughout. A slight hyaline marginal ridge less than 1 μm tall extending from elevation to elevation in the shorter specimens but not reaching the elevations in the longer ones. Mantle vertical, *c.* 5 μm deep, hyaline. Central area circular, 20–27 μm in diameter. Areolae 0.25–0.75 μm in diameter, irregularly scattered and 5–10 in 10 μm over most of the valve, in longitudinal or radial striae close to the apices, striae and areolae 16–18 in 10 μm. Periplekton with a stem slightly elliptical transversely, *c.* 4.5 × 4.0 μm, 10–12 μm tall, appressed to that of the sibling valve; ring 13–20 μm in diameter, with a continuous flange 2–3 μm broad extending for nearly 180° on either arm, clasping the stem of the sibling periplekton closely or with a gap up to 4 μm wide to one side of the valve; arms unequal, the shorter arm extending for *c.* 180°, appressed to the sibling valve throughout and with a domed or sub-spherical tip, the longer arm extending for almost 360°, appressed to the sibling valve for *c.* 180°, then narrowing and sloping towards the valve from which the periplekton arises; line joining the centres of the stems of sibling periplekta at 10°–30° to the apical axis. Ocelli 3–5 μm in diameter, transverse, vertical or almost so, porelli *c.* 55 in 10 μm. Marginal spines *c.* 4 μm tall, expanded above on the central portion, pointed and curved towards the apices on the projections of specimens with these, extending almost to the apices, 3–4 in 10 μm, inset 2.5–4.0 μm from the margin of the valve face. Superficial spines 3–4 μm tall, pointed, scattered in a band across the valve on the distal part of the central portion and the proximal part of the projections. Mature cingulum consisting of five open copulae; valvocopula with a pars exterior *c.* 7 μm deep; copula II with a pars exterior *c.* 4.5 μm deep and a well developed ligula; copula III with a pars exterior *c.* 2.5 μm deep and a well developed ligula; copula IV with a pars exterior *c.* 1.5 μm deep and a well developed ligula; copula V with a pars exterior *c.* 1.0 μm deep and a well developed ligula; the valvocopula and copulae II–IV with areolae in short vertical striae on the advalvar part of their partes exteriores, the striae and areolae *c.* 30 in 10 μm.

Late Oligocene. Komandorsky Islands, Russia (BM SEM 101590–101592; Gladenkov, 1991 and personal communication).

Navarin Basin, Bering Sea, 56° 12.3′N, 171° 42.2′W, 2500–2700 m depth. U.S.G.S Research Vessel S.P. Lee, cruise L5-78-BS, dredge sample 2-4 (BM SEM 65830–65831, B372–B375, B378–B379).

74

75
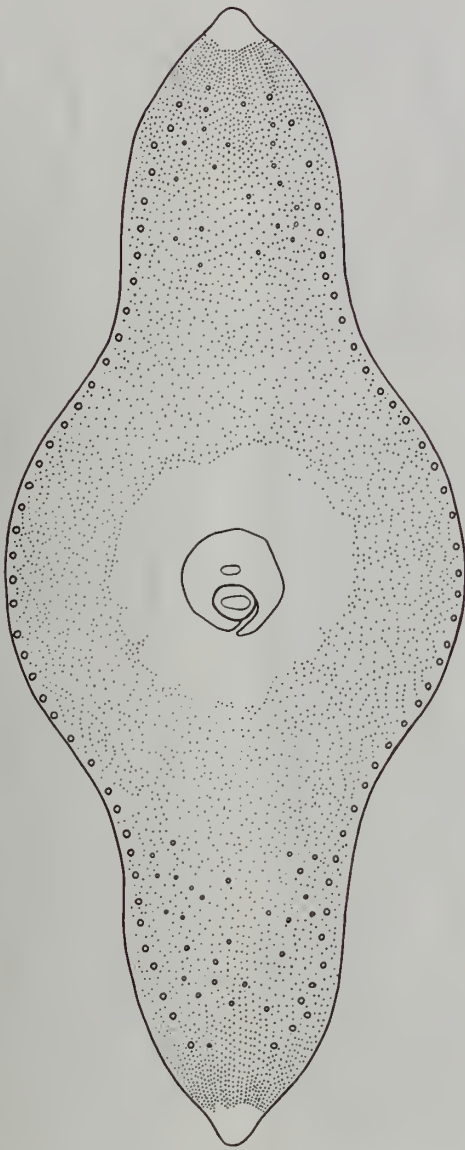
Figs 74–75 *Rutilaria obesa*, valve view, × 1000, BM 10407, Monterey, Monterey County, California, U.S.A., neotype.

Miocene. [Redondo, Alto Alentejo Province, Portugal. (BM coll. Adams J5185).]

Tokyo-wan, Honshu, Japan. (G, coll. Brun 2815bis, syntype of *R. capitata*).

Miocene–early Pliocene. Japan. (BM 8097, 8098, 9286 (syntype of *R. capitata*?); PC coll. Le Tourneur s.n.).

Hokkaido, Japan. (BM 31375, 56684, 56924, 56925, 56930, 70926, 70927, 70929, 70930, 70931, coll. Adams GC2704; PC coll. Petit s.n.).

Hakodate, Oshima, Hokkaido, Japan. (BM SEM 73349–73355).

Early Miocene. Aleutian Basin, Bering Sea, 54° 47′ 20″ N, 179° 08′ 00″ W, 1670 m depth. U.S.S. Albatross Station

4029H (BM coll. Adams M45, TS481, TS547; US 5234, 5235).

Middle Miocene. Tsubone, Suzu, Ishikawa Prefecture, Honshu, Japan. (Ichikawa, Fuji & Bachmann, 1964).

Abashiri, Hokkaido, Japan. (BM 14871 (= Tempère & Peragallo, Diatomées no. 617), 41670, 68797 (= Tempère & Peragallo, Diatom. Monde ent. no. 448), 68798 (= Tempère & Peragallo, Diatom. Monde ent. no. 449), coll. Adams TS97; BRM H.t.34).

Yabitô, Abashiri, Hokkaido, Japan (Tsumura, 1964).

Middle Miocene–late Miocene. 'Santa Lucia, California', presumably from an outcrop on the eastern side of the Santa Lucia mountains, Monterey County, California, U.S.A. (BM
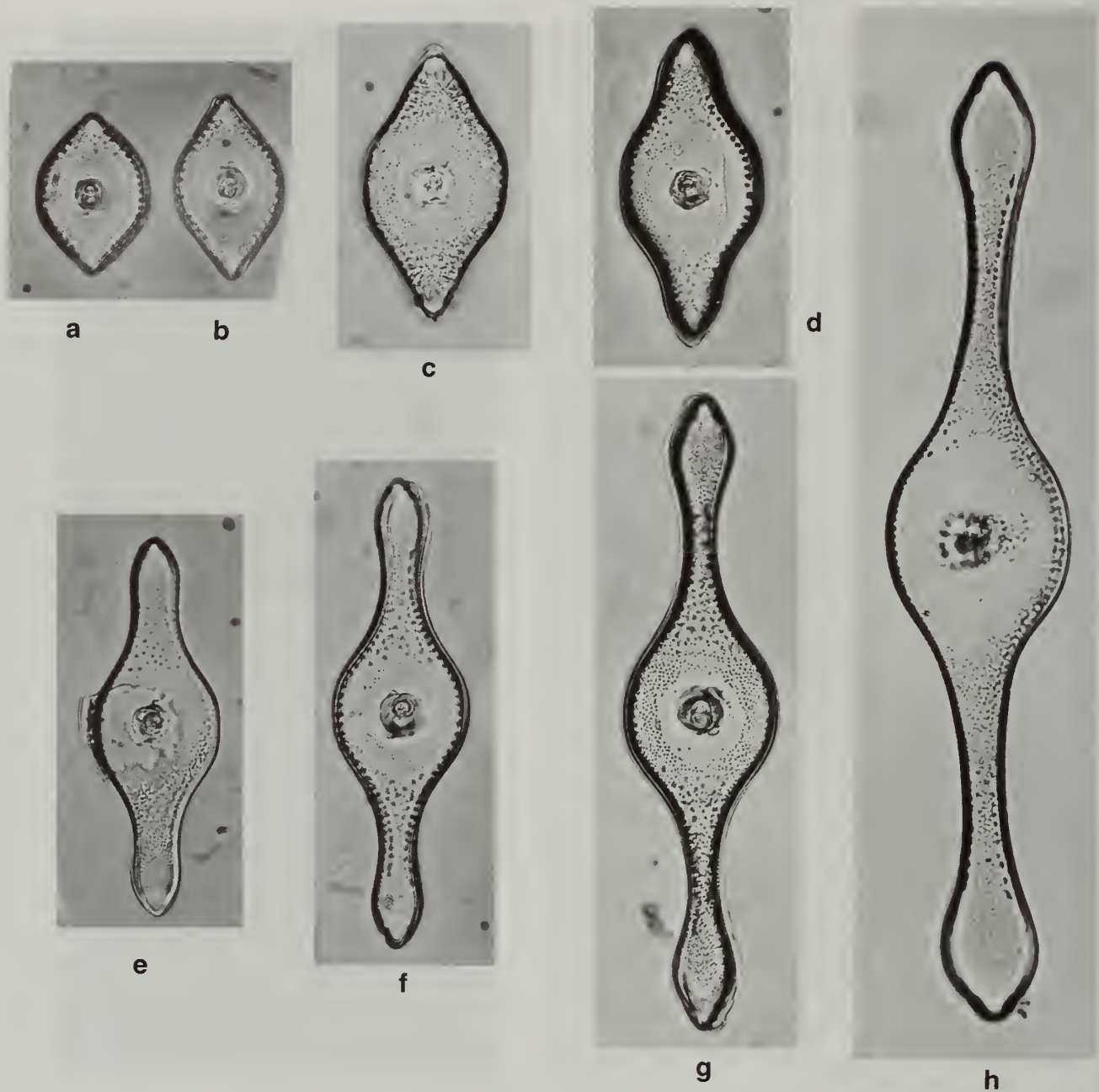
Fig. 76 *Rutilaria obesa*, specimens in valve view showing outline variation, × 500, Sendai, Miyagi Prefecture, Honshu, Japan; a,b: BM 34283, c: BM 9282; d: BM 41669; e: BM 8097; f: BM 8097; g: BM coll. Adams GC2705; h: BM coll. Adams GC2705.

14813 (= Tempère & Peragallo, Diatomées no. 559), 14814 (= Tempère & Peragallo, Diatomées no. 560), BM 69193 (= Tempère & Peragallo, Diatom. Monde ent., no. 842), BM 69194 (= Tempère & Peragallo, Diatom. Monde ent., no. 843)).

Newport Beach, Orange County, California, U.S.A. (Barron, 1975).

Middle Miocene–early Pliocene. California, U.S.A. (BM coll. Adams Bess.1758).

Mckittrick, Kern County, California, U.S.A. (Tsumura, 1964).

Late Miocene. Sendai, Miyagi Prefecture, Honshu, Japan. (BM 8147, 9282 (syntype of *R. hexagona* var. *cornuta?*), 9285, 15470, 31300, 31387, 31570, 31572, 31573, 31575,

31577, 31579, 31581, 32860, 32861, 33256, 33257, 34282, 34283, 41669, 41671, 41672, 44001, 52888, 52892 (syntype of *R. capitata?*), 52903, 52905, 54893, 54894, 60827, 60828, 60829, 60830, 60831, 63392, 63394, 68368 (= Tempère & Peragallo, Diatom. Monde ent. no. 22), 70418, 70936, 70940, 70951, 70952, 74134, 74135, 74136, 74137, 74138, 74148, 76337, 76339, 76340, 76341, 76343, 78183, 78223, coll. Adams Bess.505, Bess.506, Bess.681, C492, C498, F1089, G317. G318, GC2705, GC2707, J563, J564, J567, J2839, J4572, TS267, TS268, TS463, TS464, coll. Morley Jones s.n., s.n., s.n., s.n., SEM 66190–66196, 72824–72829, 73073–73080; BRM H.t.23, H.t.35, Zt.1.28, I.34, I.35, I.36; G, coll. Brun 2815 (syntype of *R. capitata*), 2816bis (syntype of *R. hexagona* var. *cornuta*); PC coll. Le Tourneur s.n.; PH Gen. coll. 35279, 35289, coll Shulze arr. 897, coll. Boyer G-3-19, Q-3-5,

Q-3-6, S-4-10, U-1-11, W-1-10; US 6093, 6096.)

Salinas, Monterey, Monterey County, California, U.S.A.(BM coll. Adams M649).

Monterey, Monterey County, California, U.S.A. (BM 10407 (neotype), 45566, 53378; PC coll. Le Tourneur s.n.).

4 miles east of Monterey, Monterey County, California. CAS locality 866. (CAS 216043).

Malibu, Los Angeles County, California, U.S.A. (BM SEM 97780–97787).

Temescal Canyon, Santa Monica, Los Angeles County, California, U.S.A. (BM coll. Adams TS654, SEM 80759–80768).

Malaga Cove, Los Angeles County, California, U.S.A. (Specimens labelled Redondo Beach, San Redondo and Santa Monica are included here, see Hanna, 1928b, 1936.) (BM 7335, 7336, 7337, 7977, 9281, 9949, 9959, 11022, 12924, 14448 (= Tempère & Peragallo, Diatomées no. 194), 14449 (= Tempère & Peragallo, Diatomées no.195), 31293, 31295, 31296, 32767, 32768, 32772, 32773, 32822, 33237, 33238, 33239, 33240, 33242, 33247, 33248, 33249, 33250, 33251, 35657, 41668, 45138, 45785, 45800, 45802, 45807, 45808, 45819, 54319, 54320, 54321, 55034, 55080, 55081, 55745, 56962, 56977, 60836, 60837, 63393, 64665, 64666. 64747, 66581, 66582, 68392 (= Tempère & Peragallo, Diatom. Monde ent. no. 46), 68393 (= Tempère & Peragallo, Diatom. Monde ent. no. 47), 68458 (= Tempère & Peragallo, Diatom. Monde ent. no. 112), 70957, 70964, 70965, 70973, 70981, 70985, 70986, 70989, 70990, 71000, 71002, 71006, 74140, 74950, 76342, 76344, 76345, 91035, 91036, coll. Adams A123, Bess.1568, F1091, F1092, G488, G489, G636, GC2711, GC2716, GC2717, H214, J565, J1572, J1573, J1623, J3857, TS1, TS116, TS478, coll. Bastow 854, coll. Morley Jones s.n.; BRM H.t.24, H.t.25, H.t.26, H.t.27, H.t.28, H.t.29, H.t.30, H.t.31, H.t.32, N.14.53; G, coll. Brun 1197*, 4323; MANCH coll. Chaffers B30; PC coll. Le Tourneur s.n., coll. M. Vincent A 40, A 50; PH Gen. coll. 8394, coll. Febiger 249, 260, 526, coll. Shulze arr. 1104, 1771, 2137, 2138, 2139, coll. Boyer 1082, 1083, R-1-10; US 6004, 6005, 6006.)

Palos Verdes, Los Angeles County, California, U.S.A. (BM 78182, SEM B3.45–46, B3.423–426; BRM H.t.33).

Channel Road, San Pedro, Los Angeles County, California, U.S.A. (CAS 101050).

Los Angeles, Los Angeles County, California, U.S.A. (BM coll. Morley Jones s.n.).

Late Miocene–early Pliocene. Ajigasawa, Aomori Prefecture, Honshu, Japan. (BM SEM CB14.580–581, CB14.588–596, CB19.870–877).

Sado-shima, Japan. (PC coll. Le Tourneur s.n.).

Setana, Hiyama, Hokkaido, Japan (BM coll. Morley Jones s.n.).

Embetsu, Rumoi, Hokkaido, Japan. (BM 14785 (= Tempère & Peragallo, Diatomées no. 531 as 'Wembets')).

Teshio, Rumoi, Hokkaido, Japan. (Pantocsek, 1892, 1905, as 'Thesiogori' or 'Theshiogori').

Santa Maria, Santa Barbara County, California, U.S.A. (BM 14372 = (Tempère & Peragallo, Diatomées no. 120), 31557, 45541, 74141; G, coll. Brun 1197†).

Middle Pliocene. Rekinnika Bay, Kamchatka, Russia

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* Two slides in Brun's collection have this number. See also under Santa Maria below.

† Two slides in Brun's collection have this number. See also under Malaga Cove above.

(Sheshukova-Poretskaya, 1967).

The protologue of *Rutilaria obesa* reads as follows:

> Mr Kitton writes to me in a letter about a new species of *Rutilaria* from the Californian deposits, *Rut. obesum* [sic] Grev. Mpt. The valve has 3 inflations, the central being the largest; the apices are shortly cuneate; one third of the area is smooth, the remainder distinctly covered with irregular markings. The central nodule consists of a nebulous circular spot, upon which is placed a short spiral (?) ring. Margin distinctly punctate. Mr Kitton has seen about half a dozen specimens of this species, all frustles [sic], and in no case was he able to separate the valves. I crushing partially one specimen in balsam, he observed that the nebulous central nodule was the base of a siliceous isthmus, connecting the two valves.

From this it is clear that Cleve based the description of this species on information contained in the letter from Kitton and that he himself had not seen any specimen or figure of it. The 'I' at the beginning of the last sentence is obviously a misprint for 'In'. The latest revision of the *International code of botanical nomenclature* (Greuter et al., 1994) provides that the type of a name of a species must be either a specimen or a figure. The original material of *R. obesa* contains neither of these. The name is nevertheless validly published under Art 32.1 of the Code; it is effectively published, has the correct form except for the false concord which has to be changed (see Art. 32.6), is accompanied by a description, and complies with such of the provisions of Arts 33–45 as are relevant. There is also no question as to its application.

Greville prepared, but never published, a description and figure of *Rutilaria obesa*. These are preserved in BM. The drawing is annotated 'H. Monterey 54' and the small paper folder in which the drawing and the draft description are enclosed is labelled 'Hardman–Monterey 54'; this indicates that the specimen described and illustrated by Greville was lent to him by Hardman. BM 10407 is a slide mounted by Hardman, labelled by him '*Rutilaria obesa* Monterey' and numbered by him 514; he retained it in his collection, which he had clearly re-numbered later than 1866, the year of Greville's death. The specimen on it exactly matches Greville's drawing; it is undoubtedly its original. This specimen is illustrated as Figs 74, 75 of this paper, and also by Williams (1988: pl. 53 figs 8, 9). At some time before 1881, Kitton must have seen Greville's description and figure and identified other specimens from California as Greville's unpublished species. As there is nothing that could be a holotype or a lectotype, a neotype must be chosen, and the obvious candidate is the specimen to which the name was first given, BM 10407. The statement by Williams (1988) that this specimen is the holotype of the name is an error.

There is no indication by Brun that any specimen in his collection is the holotype of either *Rutilaria capitata* or of *R. hexagona* var. *cornuta*. There are specimens named *R. capitata* by him on his slide no. 2815 from Sendai and others on his slide no. 2815bis from Yedo (Tokyo-wan). These must be regarded as syntypes of that name. There are also specimens named by him *R. hexagona* var. *cornuta* on his slide no. 2816bis from Sendai and these too are syntypes. Whether any of the slides mounted by Tempère from Sendai were prepared before the publication of these names and are thus also syntypes is uncertain, but BM 9282 is a possible syntype of *R. hexagona* var. *cornuta* and BM 9286, BM 52892 and BM 60830 are possible syntypes of *R. capitata*.

Most of the Californian specimens of *Rutilaria obesa* are smaller than the neotype and are without projections; a few are broadly lanceolate but in general they are sub-hexagonal in outline. It is not immediately obvious that Cleve's protologue applies to the species to which such specimens belong, and it is thus not surprising that Grunow (in Van Heurck, 1883) regarded one such as representing a new species, which he called *R. hexagona*.

The Japanese specimens of *Rutilaria obesa* have a continuous range of variation in outline of the valve from subhexagonal specimens 50 μm long and 32 μm broad to specimens 310 μm long and 60 μm broad with long capitate projections (Fig. 76). Examination of a large number of specimens makes it plain that there can be no taxonomic separation within this group. Even although they separated the specimens with long capitate projections from those with short projections as *Rutilaria capitata* and *R. hexagona* var. *cornuta* respectively, Brun & Tempère (1889) recognized this, saying of them and *R. longicornis* Brun & Tempère, a synonym of *R. epsilon* Greville:

> Du reste, ces trois formes de *Rutiariées* passent, dans ces calcaires, insensiblement de l'une à l'autre et il est bien difficile de leur fixer exactement des caractères-limites.

It is surprising that they included the more slender *R. epsilon*, which has a very distinct periplekton, but the remark certainly applies to the other two.

Pantocsek (1892, 1905), when examining fossil material from Japan, found specimens closely resembling those called *Rutilaria hexagona* var. *cornuta* by Brun & Tempère (1889) but considered that they represented a separate species, which he called *R. kerneri*. Grunow also, it would appear, considered that the taxon called *R. hexagona* var. *cornuta* by Brun & Tempère was a distinct species and communicated this opinion to Brun, who agreed with him. In his comments on Pantocsek's work (in Tempère, 1893), Brun says that *R. kerneri* Pantocsek is '*R. cornuta* Grunow', a new combination based on *R. hexagona* var. *cornuta* Brun & Tempère. *R. cornuta* would, of course, be an illegitimate superfluous name were it not a combination with a legitimate basionym (Greuter et al., 1994: Art. 52.3).

The range of variation in shape is different in the Californian specimens from that in the Japanese ones. Whilst the smaller Californian specimens are indistinguishable in outline from the Japanese ones without projections, the larger ones are both broader at the centre and have broader short projections that are not subcapitate. The maximum dimensions of their valves are 170 μm long and 73 μm broad, and they do not have projections more strongly developed than the neotype, which is shown in Figs 74, 75. There are occasional exceptions to this, however. A specimen from Channel Road, San Pedro, California (CAS 101050) that is 148 μm long by 42 μm broad has capitate projections only 12 μm broad expanding at the apices to 16 μm; it is thus identical in outline to the longer Japanese specimens. Another from Malibu (BM SEM 97780–97787) is 143 μm long by 54 μm broad and has very slightly subcapitate projections that are 17–18 μm broad. In addition, I have seen two specimens from Malaga Cove (PH coll. Shulze arr. 2138; BRM H.t.29) with subcapitate projections about 25 μm broad and each as long as the central portion of the valve; the projections of these are considerably broader than in any Japanese specimen with projections of comparable length.

Just as there are very occasional Californian specimens with an outline similar to that found in the larger Japanese specimens, so also specimens resembling the larger ones from California occur very rarely in the Japanese deposits. One from Sendai (BM coll. Adams Bess.506) is 111 μm long and 50 μm broad with tapering projections 27 μm broad at their base.

In all the Japanese specimens of *Rutilaria obesa* the ring of the periplekton clasps the stem of its sibling closely. In most, but not all, of the Californian specimens there is a gap of 2–4 μm between the longer arm of the ring and the stem of its sibling. Occasional specimens resembling the Japanese ones in this feature are, however, present in all the Californian localities from which I have seen a considerable number. The distribution of variation both in the outline of the valve and in the closeness with which the ring of the periplekton clasps the stem of its sibling makes it impossible to recognize any taxonomic distinction between the Californian and Japanese representatives of this species.

Too few specimens have been seen from the other localities where the species has been found for the range of variation in these deposits to be known. However, there are specimens from both the Navarin Basin and from Albatross station 4029H with short but definite projections, although none with long sub-capitate to capitate projections have been found. The one specimen from the Komandorsky Islands that I have seen has very short projections, but photomicrographs of others sent me by Dr A.Yu. Gladenkov of the Institute of the Lithosphere, Moscow, show not only similar specimens but also others with longer, subcapitate projections. It thus seems probable that the range of variation in outline of the species in the Bering Sea area was similar to that in Japan.

The species that *Rutilaria obesa* most closely resembles is *R. epsilon* Greville. In both of them the areolae, except near the apices, are irregularly scattered and are about 10 in 10 μm; the marginal spines in the central part of the valve are laterally expanded above but abut those of the sibling valve without interlocking. In *R. epsilon* there are tubercles on the outer side of the marginal spines in the central part of the valve, but these are not present in *R. obesa* (compare Plate XIX (b) with Plate XX (b), (c), (d)), nor does it have the protrusions along the upper margin of the ocellus that are present in *R. epsilon* (compare Plate XIX (d) with Plate XX (f)). Both species have large periplekta with an outer flange on the ring, but the shape of the shorter arm is very different. In *R. obesa* this encircles the stem of the sibling periplekton for about 180° and there is no hook at its tip (Plate XX (b), (d)), whilst that of *R. epsilon* diverges from the stem of the sibling periplekton and has a hook at its tip that engages with the tip of the longer arm of the sibling periplekton (Plate XIX (c)). In both species, however, there is a dome-shaped thickening of the shorter arm close to its tip. The longer arms of the periplekta of the two species are much more similar; both encircle the stem of the sibling periplekton and are appressed to the sibling valve for about 180°; they then continue as a branch that slopes down to the valve from which they arise. In spite of their differences, the periplekta of the two species resemble one another much more than they do those of any other species.

Rutilaria obesa is very readily recognized. *R. epsilon* is the only other species with a periplekton of comparable size that has an outer flange to its ring. The other species with flanges on their periplekta are all appreciably narrower than *R. obesa* and have smaller periplekta with a gap in the flange between

the two arms. All those with valves as wide as those of *R. obesa* have periplekta with equal arms and no flange and their areolae are arranged in obvious radial striae, not irregularly distributed as in *R. obesa*.

The earliest occurrence of *Rutilaria obesa* is in the late Oligocene of the Navarin Basin of the Bering Sea and of the Komandorsky Islands. It is not uncommon in the Miocene and early Pliocene deposits of Japan and California, and it occurs in the Miocene material dredged by U.S.S. Albatross at station 4029H in the Bering Sea. Sheshukova-Poretskaya (1967) records it, as *R. hexagona* var. *cornuta*, from the middle Pliocene of Kamchatka, but this record is based on a single fragmentary specimen consisting of a small part of the central portion of the valve and a subcapitate projection almost 50 μm long and 12 μm broad expanding to 14 μm. Sheshukova-Poretskaya's (1967: tabl. XLI fig. 3) illustration of this fragment suggests strongly that it is *R. obesa* but one cannot be quite certain. She does not record *R. obesa*, however, from the earlier deposits in Kamchatka and in Sakhalin where she found *R. epsilon*, nor is it recorded by Kozyrenko & Sheshukova-Poretskaya (1967) from the middle and late Miocene of the Kuril Islands where they found *R. epsilon*. Sheshukova-Poretskaya's (1967) record of *R. kerneri* from the Anadyr River, Eastern Siberia, Russia, in material dated as from about the Eocene to Oligocene boundary is, however, based on misidentified *R. hannai* R. Ross (see p. 26 above).

There is a very doubtful record from Redondo, Portugal. Reasons are given above (p. 3) for considering that the locality on the label of this specimen is an error for Redondo Beach or San Redondo, California, and that the specimen thus came from the upper Miocene of Malaga Cove, California.

Cleve's (1901) record of *Rutilaria hexagona* from a plankton gathering from Bali Sound, Indonesia, is not accompanied by a figure. It is, however, almost certainly based on a misidentification of *R. philippinarum* Cleve & Grove (see p. 51 above).

Although it shows very little detail, there can be no doubt that Laporte & Lefébure's (1930) figure identified as *Rutilaria elliptica* depicts a specimen of *R. obesa*. The outline, the disposition of the spines, and the appearance of the central process make this clear. These authors quote for each species the localities from which it has been recorded in the literature and accordingly their statement that the species they illustrate comes from Barbados does not constitute a record of *R. obesa* from the fossil deposits there.

Thus all the records of *Rutilaria obesa*, except those that are very doubtful or certainly erroneous, are from the upper Oligocene to the middle Pliocene of the northern Pacific Ocean and the surrounding shores. This distribution is almost identical with that of *R. epsilon*, except that the earliest record of that species is from the early Oligocene of the region and it has not been found later than the Miocene to Pliocene boundary.

INSUFFICIENTLY KNOWN SPECIES

Rutilaria sp. A

Rutilaria epsilon sensu Schrader & Fenner in *Initial Rep. deep Sea Drilling Proj.* **38**: 998, pl. 37 fig. 15 (1976), non Greville.

Rutilaria sp. 1 Schrader & Fenner in *Initial Rep. Deep Sea Drilling Proj.* **38**: 998 (1976).

Valve slightly inflated at the centre, otherwise linear, 95 μm long, 10 μm wide at the centre, 7 μm elsewhere. Central area circular, 4 μm in diameter. Areolae *c*. 0.3 μm in diameter, irregularly distributed, 7–8 in 10 μm. Marginal spines extending to the apices, in two rows throughout, 5 in 10 μm.

Oligocene. Iceland–Faeroe ridge, north Atlantic, 56° 21.06'N, 07° 47.27'W, 811 m depth. Deep Sea Drilling Project Hole 336, 18-2 (55–57) (Schrader & Fenner, 1976).

The brief description given above is based on the figure in Schrader and Fenner's paper cited above. Both the entries cited refer to the same figure. They are obviously an unintentional duplication, but it is impossible to say whether this is because the authors were originally unable to identify the specimen figured and then decided it was *Rutilaria epsilon*, or vice versa. It is clearly not *R. epsilon* nor any other described species of *Rutilaria*. It is closest to *R. schenkii* R. Ross, but differs in having a much shorter central portion to the valve and broader projections with the marginal spines in two rows throughout. It almost certainly represents an undescribed species, but one that is not sufficiently known to be given a name.

Rutilaria sp. B

Rutilaria areolata sensu Schrader & Fenner in *Initial. Rep. deep Sea Drilling Proj.* **38**: 998 pro parte, quoad pl. 37 fig. 16 (1976), non Sheshukova-Poretskaya.

Valve with strongly convex margins at the centre tapering sharply into subcapitate projections, *c*. 60 μm long and 16 μm broad. Central area circular, diameter *c*. 7 μm. Areolae large, diameter *c*. 0.5 μm, in short radial striae opposite the central area, elsewhere irregularly arranged, striae 8–9 in 10 μm, areolae 5–6 in 10 μm. Marginal spines 4–6 in 10 μm, in a single central line on the projections, without any longitudinal extensions.

Oligocene. Iceland–Faeroe ridge, north Atlantic, 56° 21.06'N, 07° 47.27'W, 811 m depth. Deep Sea Drilling Project Hole 336, 18-2 (55–57) (Schrader & Fenner, 1976).

The single specimen described above is figured in the same paper by Schrader & Fenner (1976) as *Rutilaria* sp. A and comes from the same core sample. The two resemble each other, and also *R. minima* subsp. *danica* R. Ross, *R. areolata* Sheshukova-Poretskaya subsp. *areolata* and *R. schenkii* R. Ross, in the size and spacing of their areolae. *R. minima* subsp. *danica* differs from all the others of these in having no marginal spines. *R. areolata* subsp. *areolata* and *R.* sp. B have a subcircular central portion to their valves and also a single central row of marginal spines on their projections. The photomicrograph of *R.* sp. B, however, shows quite clearly that its distal marginal spines do not have any longitudinal

costate extensions. Apart from its outline, *R.* sp. B resembles *R. schenkii* more closely than it does *R. areolata* subsp. *areolata*. There is very considerable variation in outline in a number of species of *Rutilaria*, but in all of them the shape of the central portion varies little. It therefore seems unlikely that the specimen treated here as *R.* sp. B is within the range of variation of *R. schenkii*. Also, the arrangement of the distal marginal spines, whether in two rows or a single central row, is usually constant within a species. *R.* sp. A and *R.* sp. B differ in this as well as in the shape of the central portion and accordingly, although they occurred in the same sample, it seems unlikely that they belong to the same species.

Rutilaria sp. C

Rutilaria sp. Barron & Mahood in *Micropaleontology* **39**: 42, pl. 5 fig. 5 (1993).

Valve 40 μm long, 8 μm broad, with a central portion with convex margins and subcapitate projections 3 μm broad expanding to 4 μm at the acute apices. Periplekton apparently very small, its ring only *c.* 2 μm in diameter. Marginal spines *c.* 8 in 10 μm, extending to the apices. Scattered superficial spines.

Early Oligocene. Prydz Bay, Antarctica. Ocean Drilling Program Hole 739C, 30R–1, 108 cm (Barron & Mahood, 1993).

The description given above is based on the photomicrograph of the single specimen of *Rutilaria* found by Barron & Mahood (1993) in the lower Oligocene material from Prydz Bay, Antarctica, recovered from Ocean Drilling Program Hole 739C. Whilst this photomicrograph, of which I have seen direct prints, does not show any areolae or striae, there are indications that some are present. This specimen clearly belongs to a different species from any known from elsewhere. The outline is similar to that of the longer specimens of *R. barbadensis*, *R. elliptica* and *R. philippinarum*, but it is much smaller than these, and its superficial spines are arranged differently from those of *R. philippinarum*, the only one of these species to have superficial spines.

Fenner (1981: pl. 29 fig. 11) also records and figures an unnamed species of *Rutilaria* from an upper Oligocene sample from Deep Sea Drilling Project Hole 369A just off the coast of Morocco, 26° 35.5′N, 14° 59.0′W, 1752 m depth. This figure does not show sufficient detail for identification. The valve is broadly elliptical with very slight projections at the apices, 22 μm long, 10 μm broad; no areolae can be seen; there are marginal spines about 5 in 10 μm not interrupted opposite the central area, and there is an indication that the most distal of these are extended longitudinally to form costae. It is possible, therefore, that this diatom is a very small specimen of *R. tenuicornis* subsp. *paleogena* R. Ross.

Schrader (1978) records an unnamed species of *Rutilaria* as occurring rarely in one sample only from Deep Sea Drilling Project Hole 366 drilled on the Sierra Leone Rise in the eastern tropical Atlantic, 5° 40.07′N, 19° 51.01′W, 2853 m depth. It was found in the sample core 15–1, 22–23 cms, which comes from the early part of the Late Eocene, but as there is no illustration, one cannot know what species was found there.

SPECIES EXCLUDENDAE

Rutilaria recens Cleve in *K. svenska VetenskAkad. Handl.*, Ny Földj **18**(5): 19, pl. IV fig. 57 (1881).
≡ *Rutilariopsis recens* (Cleve) Van Heurck, *Treat. Diatom., transl. Baxter*: 60 (1896).

Rutilaria lanceolata sensu J.D. Möller, *Diatom.-Präp.*: Taf. 26 Reihe 6 no. 28 (1891); *Verz. Lichtdrucktaf. Möll. Diatom.-Präp.*: 165 (1892), non Grove & Sturt.
Indeterminable, not *Rutilaria*.

Rutilaria kertschiana Missuna in Proshkina-Lavrenko et al, *Diatom. Analiz* **2**: 216, tabl. 99 fig. 11 (1949).
Not *Rutilaria*, probably *Cestodiscus rhombicus* Grunow in Van Heurck, *Syn. diatom. Belgique*: pl. 129 fig. 3 (1883).
Cestodiscus rhombicus Grunow, from the Miocene of Naparima, Trinidad, is normally regarded as a synonym of *Coscinodiscus rhombicus* Castracane, a recent species from the Sea of Japan, but this is probably an error.

Rutilaria sp. E. de S. Silva in *Mems Jta Invest. Ultramar*, ser. 2, **18**: 27, Est. XII figs 3, 4 (1960). '*Rutilaria eliptica*'[sic] in table opposite p. 40.
Not *Rutilaria*, apparently *Glyphodesmis*.

Rutilaria antiqua Strelnikova, *Diat. pozdnego Mela (Zapad. Sibir')*: 109 (1974).
≡ *Strelnikovia antiqua* (Strelnikova) Ross & Sims in *Bull. Br. Mus. nat. Hist.* (Bot.) **13**: 326 (1985).

Rutilaria sp. Strelnikova, *Diat. pozdnego Mela (Zapad. Sibir')*: 109 (1974).
≡ *Strelnikovia tumida* (Strelnikova) Ross & Sims in *Bull. Br. Mus. nat. Hist.* (Bot.) **13**: 327 (1985).

Rutilaria tenuis sensu Glezer in Glezer et al., *Diatom. Vodor. SSSR* **1**: 111, tabl. XV fig. 14 (1974), non Assimova, nom. invalid., nec *Rutilaria tenuis* (Grove & Sturt) Brun & Tempère (1889).
Spinovinculum inzensis R. Ross in *Beih. Nova Hedwigia* **100**: 268 (1990).

Syndetocystis uralensis Strelnikova, *Diat. pozdnego Mela (Zapad. Sibir')*: 79 (1974).
Not *Rutilaria*. This species belongs to an undescribed genus. The large central oblique process is a rimoportula (P.A. Sims, personal communication). It may be a precursor of *Rutilaria*, but this is unlikely as there is no trace of ocelli or structures that might give rise to these.

DISCUSSION

During the twenty-five years that it has been available, the scanning electron microscope has shown us the structure of the frustule of diatoms in much more detail than we could see with the light microscope. This increased knowledge has made it obvious that the previously accepted classification of the Bacillariophyceae, originally formulated by Schütt (1896) and later revised by Karsten (1928), had to be replaced by a substantially different one. There is, however, no consensus about the changes that should be made. Three appreciably different classifications have been put forward in recent years (Simonsen, 1979; Glezer et al, 1988; Round, Crawford & Mann, 1990). In all of these the centric diatoms as a whole

form one of the major groups, although this is given a different rank, and a different name, in each. In Simonsen's (1979) classification the lowest rank recognized above genus is the subfamily, and one of his subfamilies is the Rutilarioideae, in which he includes *Rutilaria* Greville, *Syndetocystis* Greville and *Syndetoneis* Grunow. The lowest rank above genus recognized by Round, Crawford & Mann (1990) is the family, and one of their families is the Rutilariaceae, including only *Rutilaria* and *Syndetocystis*; they do not treat *Syndetoneis* as a separate genus. Glezer et al. (1988) also recognize no rank between genus and family; in their classification there is a family Rutilariaceae consisting of *Rutilaria* and *Kisseleviella* Sheshukova-Poretskaya; *Syndetocystis* and *Syndetoneis* are not mentioned in this classification. There is thus agreement between the authors of these three classifications that *Rutilaria*, as delimited here, is a genus with no close relatives, except for the suggestion by Glezer et al. (1988) that it should be grouped with *Kisseleviella*. The detailed description and illustrations of that genus provided by Akiba & Yanagisawa (1985) show, however, that the two genera have not got nearly enough in common to be placed in the same family. Apart from the possibility that *Kisseleviella* may be closely related to *Spinivinculum* R. Ross (1990), its affinities are very obscure.

Glezer (1984), when describing the monotypic new genus *Trochosiropsis* Glezer based on *Trochosira mirabilis* Kitton, called the central linking mechanism of this species a periplekton, and suggested that *Trochosiropsis* might be closely related to *Rutilaria* and *Syndetocystis*. Sims (1988), however, subsequently showed that the structure in *Trochosira mirabilis* is not a rimoportula. It is thus not homologous with the periplekton of *Rutilaria*. *Trochosiropsis* is not listed in the classification put forward by Glezer et al. (1988), but it is included in the continuation of the work in which this appeared (Glezer et al., 1992). In this it is described by Glezer, who does not use the term periplekton for its central linking mechanism and no longer suggests that it may be closely related to *Rutilaria*.

There is much less agreement about the position of the Rutilarioideae or Rutilariaceae within the classification of the Bacillariophyta than there is about the content of the family. In Simonsen's (1979) classification the Eupodiscaceae comprises two subfamilies, the Eupodiscoideae, which includes all the genera with well developed ocelli, and the Rutilarioideae, in which the ocelli are less well developed. This family is one of the four which he includes in the suborder Biddulphiineae. Glezer et al. (1988) base their system primarily on the type of areola; they include the Rutilariaceae, along with many other families with poroid areolae, in the order Biddulphiales, placing it between the Cymatosiraceae and the Lithodesmiaceae. However, of the genera that Simonsen includes along with *Rutilaria* in the family Eupodiscaceae, Glezer et al. include only four in the Biddulphiales and place eight in other orders. Round, Crawford & Mann (1990) give the rank of class to the centric diatoms, which they call the Coscinodiscophyceae. One of the subclasses into which they divide this class is the Cymatosirophycidae, consisting of the two families Cymatosiraceae and Rutilariaceae. In their classification the Cymatosirophycidae are placed between the Corethrophycidae, a subclass containing only the one genus *Corethron* Castracane, and the Rhizosoleniophycidae. They include the Triceratiaceae, a family consisting of the genera that constitute Simonsen's (1979) Eupodiscoideae, in the Biddulphiophycidae along with the Biddulphi-

aceae, the Hemiaulaceae and various other families. Glezer et al. (1988) and Round, Crawford & Mann (1990) thus agree that the Rutilariaceae are close to the Cymatosiraceae; Simonsen (1979), on the other hand, includes *Cymatosira* Grunow and *Campylosira* Van Heurck in the Biddulphiaceae. This agreement between Glezer et al. (1988) and Round, Crawford & Mann (1990) that the Rutilariaceae and the Cymatosiraceae are closely related is the only point about the relationships of the Rutilariaceae on which any of the three classifications agrees with another.

Various criticisms can be levelled at each one of these three classifications of the Bacillariophyceae, and no one of them is likely to be accepted without considerable modification. One can say, however, that any acceptable classification would include a monotypic family Rutilariaceae; there is no other genus with sufficient similarity to *Rutilaria* for it to be included in the same family. The relationship of this family to the other families of centric diatoms is less obvious. One would expect an evolutionary precursor of *Rutilaria* to have the following characters: a bipolar valve with a single central rimoportula, elevations at the apices bearing either an ocellus or a structure that might give rise to one, marginal spines or a well developed marginal ridge. There are Cretaceous species belonging to the Hemiaulaceae that have all these characters, e.g. *Sphynctolethus monstrosus* Hanna and *Pseudoaulacodiscus jousae* Vekschina (see Sims, 1986), provided that one accepts the suggestion made by Simonsen (1979) that the ocellus is derived from the structure found on the summit of the elevations of such species as these. These members of the Hemiaulaceae are the only diatoms known from the Cretaceous or Paleocene that have all these characters and might thus be, or be closely related to, evolutionary precursors of *Rutilaria*. The possibility that *Syndetoneis uralensis* Strelnikova, the only known species of an undescribed genus, is a precursor of *Rutilaria* cannot be ruled out, but it seems very unlikely. It has a circular valve with a central rimoportula the outer part of which is a massive tube, but there is no sign of any structure that might give rise to an ocellus, nor even of any bipolarity. When considering the evolutionary history of *Rutilaria*, one must take into account the fact that its ocellus is rather less well developed than that found in those genera included by Simonsen (1979) in the Eupodiscoideae and by Round, Crawford & Mann (1990) in the Triceratiaceae. These facts are best fitted by the following assumptions about the evolutionary history of *Rutilaria*: (a) there was an evolutionary line of descent from Cretaceous members of the Hemiaulaceae to the genera with an ocellus included in the Triceratiaceae sensu Round, Crawford & Mann (1990); (b) *Rutilaria* arose as a side branch from this evolutionary line and from a representative of that line with only one central rimoportula and with an ocellus at an intermediate stage between that of the late Cretaceous precursor and that found in the Triceratiaceae.

The absence of representatives of this intermediate stage in the fossil record is not a strong objection to this hypothesis. The number of species and genera found in any one marine fossil deposit is comparable to the number of species and genera found living today in a single locality. This suggests that the diversity of the marine diatom flora as a whole was of the same order in late Cretaceous and Paleocene times as it is today, but that the small number of fossil deposits known from any one epoch means that only a fraction of the species existing at any one time appears in the fossil record as we yet know it. The flora of shallow marine environments, which are

particularly rich in species, is especially under-represented.

If the opinions about the relationships of *Rutilaria* set out in the last paragraph are accepted, the taxon of the next higher rank above family, whether suborder or order, that included the Hemiaulaceae should also include the Rutilariacae and the Triceratiaceae, with perhaps some modification of the generic content of the Hemiaulaceae and Triceratiaceae. The Cymatosiraceae Hasle, von Stosch & Syvertsen (1983) should also be included with these. This family appears considerably later in the fossil record than the Rutilariaceae and there is much to suggest that it originated either from *Rutilaria* or from one of its close precursors. The two families have bipolar valves with not very strongly developed ocelli at their apices and, in some species of each, marginal spines expanded above and interlocking. In the Cymatosiraceae also, in those valves where one is present, the rimoportula is single and close to being central. There may be other families closely enough related to the Hemiaulaceae or the Triceratiaceae to be included in this suborder or order but this is not a matter to be considered here.

Not only are the evolutionary precursors of *Rutilaria* missing from the fossil record, but there had also been considerable divergence within the genus before its first appearance. The earliest firm records are from the Paleocene. All the species known from that epoch, *R. erinaceus* R. Ross, *R. minima* R. Ross, *R. delicatula* R. Ross, *R. hyalina* R. Ross, and *R. hustedtii* R. Ross, have periplekta in which the tips of the arms are bent back towards the valves to which they are attached; this prevents the rings of the periplekta sliding up and down on the stems of their siblings. This is the case in all other species of *Rutilaria* except for *R. grevilleana* (Walker & Chase) R. Ross, which first appears in the early Eocene, and *R. amplectans* (Grove & Sturt) R. Ross, the first firmly dated record of which is from near the middle to late Eocene boundary. Not only do these two species have simpler periplekta than the others in the genus, they also have prominent elevations and valves with elliptical to circular outlines without projections. These latter characters occur in the diatoms which are suggested above as ancestral to the genus. The indications thus are that these two species diverged from the evolutionary line that led to to the rest of the genus before the arms of the periplekta developed the form that prevented the rings from sliding on the sibling stems. The two species had themselves diverged considerably before their appearance in the fossil record. *R. grevilleana* has marginal spines but no superficial spines and large areolae arranged in radial striae, whilst *R. amplectans* has superficial spines but no marginal spines and small areolae irregularly arranged.

Rutilaria erinaceus differs from the other Paleocene species of the genus by having a periplekton with a larger ring and with equal arms. There are a number of other species that also have periplekta with a large ring and equal arms: *R. limoniformis* R. Ross, *R. kamyshlovensis* R. Ross, *R. interrupta* R. Ross, *R. radiata* Grove & Sturt and *R. hannai* R. Ross. In all of these species the areolae are arranged in radial striae with the striae further apart from one another than the areolae within them, although this is not obvious in *R. limoniformis* because the striae are very interrupted. In all the species of the genus with unequal arms to the periplekta the areolae are either irregularly arranged or are in radial striae as close as or closer than the areolae within them. The characteristics shared by these species suggest that they are a monophyletic group and that the divergence between them

and those with unequal arms occurred before *Rutilaria* first appeared in the fossil record. *R. kamyshlovensis*, however, differs from the others of this group in having interlocking marginal spines with tubercles near their bases. These characteristics are otherwise found only in species in which the ring of the periplekton is small and has unequal arms.

Although *Rutilaria erinaceus* is the first of this group of species to appear in the fossil record, it seems unlikely that it is ancestral to the others. It has no marginal spines, and the few species of *Rutilaria* which lack these are very diverse and seem related to quite different groups within the genus. From this it would seem that the possession of marginal spines was a character of the earliest members of the genus and that loss of them has occurred on a number of separate occasions during its evolution. The broadly ovate outline of the valve with no projections that this species shares not only with *R. limoniformis* but also with *R. grevilleana* and *R. amplectans* is probably a primitive character. Of the species of this group with projections, the one which appears earliest in the fossil record is *R. kamyshlovensis*, found in the early Eocene. This differs from the others in having interlocking linking spines with tubercles, which suggests a possible relationship with the group of species that includes *R. elliptica* Greville and *R. philippinarum* Cleve & Grove. These have similar marginal spines but have periplekta with small rings and unequal arms and also areolae at least as distant as the striae. However, none of the four Paleocene species that have periplekta with small rings with unequal arms have interlocking marginal spines, although *R. hustedtii* R. Ross, which seems to be ancestral to the group that includes *R. elliptica* and *R. philippinarum*, has tubercles on the marginal spines. The balance of evidence therefore suggests that *R. kamyshlovensis* is more closely related to *R. interrupta*, *R. radiata* and *R. hannai* than it is to *R. elliptica*, *R. philippinarum* and the species that are close to them. Its affinities are, nevertheless, obscure.

R. interrupta appears in the fossil record in the middle Eocene, rather earlier than *R. radiata* and *R. hannai*. It differs from these two species by having well developed apical elevations and a central portion so narrow that there are no areolae opposite its central area and also by lacking marginal and superficial spines. These differences suggest that it is not as closely related to these two species as they are to each other. The first appearances of *Rutilaria radiata* and *R. hannai* are in the late Eocene. These two differ only in the outline of their central portions, the shape of the rings of their periplekta and the closeness of their striae and areolae; they would seem to be very closely related.

The species of *Rutilaria* in which the two arms of the ring of the periplekton are unequal are more diverse than those with equal arms and they constitute a number of separate groups of species with characters in common. *Rutilaria minima* R. Ross, *R. delicatula* R. Ross, *R. hyalina* R. Ross, and *R. hustedtii* R. Ross, the four species that occur in the Paleocene deposit at Inza in the central Volga basin of Russia, have many similarities. All are small, their valves have an elliptical central portion and short projections, and their periplekta are small and have a narrow outer flange on their unequal arms. Nevertheless, the differences between them are such that they appear to be related to different groups that appear later in the fossil record.

Rutilaria minima differs from the other species found in the deposit at Inza by having no marginal spines but a costa in the position where such spines occur in other species. The Inza

specimens and those occurring in the slightly later Fur-Formation in Denmark differ slightly in outline but otherwise only in the size and spacing of the areolae, and they can thus be separated at no more than the subspecific level. There is also no more difference between the two subspecies of *R. areolata* Sheshukova-Poretskaya, another small species, but one which has marginal spines, the more distal ones extended as longitudinal costae. One subspecies of this extends from the middle Eocene to the late Eocene, the other from the late Eocene to the late Oligocene. The resemblances between *R. minima* and *R. areolata* are such as to suggest their close relationship. Whether there was a continuous range in areolar size and density in either or both of these two species one cannot tell; they are too rare in the small number of deposits in which they occur.

Rutilaria schenkii R. Ross is larger than either *R. minima* or *R. areolata*, but it has the same large areolae as *R. minima* subsp. *danica* R. Ross and *R. areolata* subsp. *areolata* and its most distal marginal spines have longitudinal costate extensions. Also, as in *R. areolata*, there are small patches of areolae on the mantle just proximal to the apices. These similarities suggest a close relationship. The two imperfectly known species, *Rutilaria* sp. A and *Rutilaria* sp. B, which also have large areolae, seem too to be related to *R. schenkii*.

Rutilaria delicatula has two parallel rows of marginal spines along each side of the valve, those in the outer row being rather smaller and closer than those in the inner one. Those in both rows are tapering and pointed, and are similar to the marginal spines found in many other species. *R. hyalina* also has two rows of marginal spines, but these are different from those in other species. Those in the inner row are cylindrical, not tapering and pointed, and they are more closely spaced than are the marginal spines of any other species of *Rutilaria*. Those in the outer row are even more closely spaced and are minute and globular. The only other species to have two parallel rows of marginal spines is *R. briggeri* R. Ross from the middle Eocene, and in this species the spines in the outer row are also very small and are not tapering and pointed like those of the inner row. It seems probable that these three species of *Rutilaria* with two parallel rows of marginal spines are closely related to one another.

Rutilaria briggeri is a species with long slender projections. The ring of its periplekton has a broad flange which is interrupted by a U-shaped gap between the two arms and its areolae are arranged in striae that are about 20 in 10 μm. These characteristics are present in two other species with first records from the middle Eocene, *R. tenuicornis* Grunow and *R. tenuis* Grove & Sturt, but these have only a single row of marginal spines along either side of the valve. Apart from the absence of the outer row of marginal spines, these two species differ from *R. briggeri* in the outline of the central portion of the valve. The main difference between *R. tenuicornis* and *R. tenuis* is that in the former, as in *R. briggeri*, there are short longitudinal costae attached to the proximal side of each elevation and the distal marginal spines have longitudinal costate extensions to their bases. *R. lanceolata* Grove & Sturt, another long slender species that is known only from the upper Eocene of Oamaru, New Zealand, has a very similar periplekton and areolae similarly arranged but rather more widely spaced, but it differs from these species in having no marginal spines. Its similarities to them, however, indicate that *R. briggeri*, *R. tenuis*, *R. tenuicornis* and *R. lanceolata* form a closely related group

derived from the earlier *R. delicatula*, *R. hyalina*, or their immediate relatives.

Rutilaria cantabrigiensis R. Ross is another species found in the middle Eocene that is very similar to *R. briggeri* in outline, in the arrangement and spacing of its areolae and in the presence of longitudinal costae on the proximal side of the elevations. Also, like *R. briggeri*, and the other species discussed in the previous paragraph, it has a broad flange on the ring of its periplekton, but this is extended away from its sibling in the form of a letter U with broad uprights that reach beyond the central area as far as superficial spines on the sibling valve. These fit into indentations in the distal edges of the extensions of the flange. Although this structure seems very different from anything found elsewhere in the genus, it is no more than a slight modification of the flange with a U-shaped gap found in *R. briggeri* and related species. *R. flabellifera* R. Ross, which may be early Oligocene or early Miocene in age, has a periplekton that is even more modified. It has only one short arm that does not encircle the stem of the sibling, but the two lobes of its flange are broader than those of *R. cantabrigiensis*, and the indentations in their outer edges apparently grasp the superficial spines of the sibling valve, thereby holding the two sibling valves together. There seems little doubt that *R. cantabrigiensis* is ancestral to *R. flabellifera* and that the two species have a common origin with the group containing *R. briggeri*, etc.

Rutilaria hustedtii R. Ross is the only Paleocene species with tubercles on the outer side of its marginal spines near their base. Such tubercles are present on the marginal spines of a number of species that appear later in the fossil record. One group of these, *R. barbadensis* R. Ross, *R. elliptica* Greville, *R. australis* R. Ross and *R. philippinarum* Cleve & Grove, all first recorded in the middle Eocene, and also *R. szakalensis* Pantocsek, from the Miocene, appear to be closely related. All of these have small periplekta without flanges on their unequal arms and striae that are closer than the areolae within them. Their marginal spines are expanded above and interlocking, whereas those of *R. hustedtii* are pointed. The presence of tubercles on the marginal spines may nevertheless indicate that *R. hustedtii* is, or is closely related to, a precursor of this group. It does not have any costae attached to the elevations, which makes it much less probable that *R. hustedtii* is related to *R. areolata* Sheshukova-Poretskaya, another species with tubercles on its marginal spines. For the same reason it is also unlikely that *R. hustedtii* is closely related to the group of species that includes *R. briggeri* and *R. tenuicornis*; although these have similar periplekta with flanges on the arms, they have distal costae but no tubercles on the marginal spines.

The only other species with tubercles on the outer side of the marginal spines is *Rutilaria kamyshlovensis* R. Ross and this also has marginal spines that are expanded above and interlocking. Although it appears in the fossil record in the early Eocene, after *R. hustedtii* and before *R. barbadensis*, *R. elliptica*, *R. australis* and *R. philippinarum*, it seems unlikely that it is phylogenetically intermediate between these. It has a large periplekton with equal arms and areolae much closer than its striae, as do also *R. interrupta*, *R. radiata* and *R. hannai*, and it is more probably related to these species, although its affinities are very uncertain.

The poorly known *R. attenuata* R. Ross, from the upper Eocene, is possibly closely related to the group of species that includes *R. elliptica*; its areolae have a similar arrangement and spacing. On the other hand, its marginal spines are

pointed and without tubercles, and it has costae attached to the elevations. This suggests that it may instead have affinities with *R. briggeri* and its relatives.

Two of the species with interlocking marginal spines, *Rutilaria philippinarum* Cleve & Grove and *R. elliptica* Greville, have a similar very wide range in the outline of their valves, from those with long subcapitate projections to those that are elliptical and without any projections. Many fewer specimens of *R. barbadensis* R. Ross and *R. australis* R. Ross have been seen, but all of these have projections; these species may thus not have the same range of outline as *R. philippinarum* and *R. elliptica*. *R. barbadensis* and *R. philippinarum* do not have raised elevations, which are present in *R. elliptica* and *R. australis*. *R. australis* and *R. philippinarum* have vertical striae on the valve mantle, whereas this is hyaline in *R. barbadensis* and *R. elliptica*. *R. philippinarum* is the only one of these four species to have superficial spines. These species obviously form a closely related group; they all have small periplekta with unequal arms without flanges, areolae more widely spaced than the striae, and interlocking marginal spines with tubercles on their outer sides. They all first appear in the middle or late Eocene. *R. szakalensis*, first recorded in the Miocene, shares the characteristics that unite this group and is clearly derived from them. It differs from them in having no projections; its valves are always broadly lanceolate in outline. Its marginal spines extend to the apices, where it has well developed elevations, characters that it shares with *R. elliptica* and *R. australis*, but it also has superficial spines, present in *R. philippinarum* but not in *R. elliptica*, *R. australis* nor *R. barbadensis*. The way in which these five species, which clearly belong together, are related to one another is obscure.

The periplekton of *Rutilaria epsilon* Greville is much larger than that of the species discussed in the previous paragraph, and it has a flange, although not a very distinct one, on the ring. It does, however, resemble *R. philippinarum* and *R. elliptica* in a number of ways. Like them, its marginal spines have small tubercles on the outer side near the base, and those in the central part of the valve are expanded above, although they apparently do not interlock but only abut. Also, the areolae of *R. epsilon*, although more irregularly arranged than in *R. elliptica* and *R. philippinarum*, are more distant longitudinally than transversely, even close to the apices where they form short longitudinal striae. *R. epsilon* appears later in the fossil record than most of the species with interlocking marginal spines and its similarities to them suggest that it is descended from that group. If this is so, however, the flange on its periplekton has presumably arisen independently from that present in the Paleocene species and the group derived from *R. delicatula*, which is discussed above.

Rutilaria obesa Cleve appears even later in the fossil record than *R. epsilon*, which it resembles in a number of ways. It has a large periplekton with a continuous flange on the ring and a shorter arm with a domed swelling near its tip; the areolae are irregularly arranged except close to the apices, where they form short longitudinal striae, and their spacing is similar to that in *R. epsilon*; the marginal spines in the central part of the valve are expanded above and abut. These resemblances are sufficient to suggest that there is a close phylogenetic relationship between *R. obesa* and *R. epsilon* and hence that *R. obesa* also is derived from the group that includes the species with interlocking linking spines.

There had clearly been considerable divergence within the genus *Rutilaria* before its first appearance in the fossil record. The species with periplekta the arms of which interlocked in such a way as to prevent the rings sliding up and down on the stem of the sibling had separated from those with simpler rings that could do this. Those with interlocked arms had divided into those species with equal arms and those with unequal arms. The one Paleocene species with equal arms is probably not directly ancestral to the later species with this characteristic; it has no marginal spines whilst most of them do. The Paleocene species with unequal arms had themselves begun to diversify, and the various groups into which the species with such periplekta are divided had apparently begun to separate.

The suggestions about the relationships between the species made above can only be put forward tentatively. This scheme, and any other that could be proposed, has to postulate that several characters emerged independently more than once. The distribution of characters set out in Table 1 makes this obvious. This uncertainty about the way in which the species are related is both evidence for the fact that the fossil record of the genus is incomplete and a consequence of that fact.

The reasons for considering that the Rutilariaceae and the

Table 1 Distribution of characters in species of *Rutilaria*.

	1	2	3	4	5	6	7	8	9
R. grevilleana	–	–	–	–	–	–	–	–	–
R. amplectans	–	–	–	+				+	–
R. erinaceus	+	–	–	+				+	–
R. limoniformis	+	–	–	–	–	–	–	+	–
R. interrupta	+	–	–	+				–	–
R. radiata	+	–	–	–	–	–	–	–	+
R. hannai	+	–	–	–	–	–	–	+	+
R. kamyshlovensis	+	–	–	–	–	+	–	–	–
R. minima	+	+	+	+				–	–
R. areolata	+	+	+	–	+	–	+	+	–
R. schenkii	+	+	+	–	+	–	+	+	–
R. delicatula	+	+	+	–	–	–	–	+	–
R. hyalina	+	+	+	–	–	–	–	–	–
R. briggeri	+	+	+	–	+	–	+	+	–
R. tenuicornis	+	+	+	–	+	–	–	+	–
R. tenuis	+	+	+	–	–	–	+	+	–
R. lanceolata	+	+	+	+				–	+
R. cantabrigiensis	+	+	+	–	+	–	–	+	–
R. flabellifera		+	+	–	+	–	+	+	–
R. hustedtii	+	+	+	–	–	–	–	–	–
R. barbadensis	+	+	–	–	–	+	–	–	+
R. elliptica	+	+	–	–	–	+	–	–	–
R. australis	+	+	–	–	–	+	–	–	–
R. philippinarum	+	+	–	–	–	+	–	+	+
R. attenuata			–	+	–	+	–		
R. szakalensis	+	+	–	–	–	+	–	+	–
R. epsilon	+	+	+	–	–	+	–	+	–
R. obesa	+	+	+	–	–	+	–	+	–

1.+ Arms of periplekton deflexed	– Arms of periplekton simple
2.+ Arms of periplekton unequal	– Arms of periplekton equal
3.+ Arms of periplekton flanged	– Arms of periplekton not flanged
4.+ Marginal spines absent	– Marginal spines present
5.+ Distal marginal spines with costate extensions	– Distal marginal spines without costate extensions
6.+ Marginal spines expanded above	– Marginal spines pointed
7.+ Distal marginal spines in a single central row	–Marginal spines in two rows throughout
8.+ Superficial spines present	– No superficial spines
9.+ No elevations	– Elevations present

Cymatosiraceae are closely related are given above (p. 66) and the relative times of their appearance in the fossil record suggests that the Rutilariaceae were probably ancestral to the Cymatosiraceae. One of the main characters that the two families have in common is the possession of interlocking marginal spines. In *Rutilaria* these are found both in the group of species which have small periplekta with unequal arms and no flange, *R. barbadensis*, *R. elliptica*, *R. australis*, *R. philippinarum*, *R. szakalensis*, and also in *R. kamyshlovensis*. The arrangement and spacing of the areolae in the Cymatosiraceae is much closer to that in the species of *Rutilaria* with small periplekta, and this suggests that the ancestor of the Cymatosiraceae came from within this group, which itself apparently arose at a comparatively late stage in the diversification of *Rutilaria*.

Rutilaria is primarily a Paleogene genus. The earliest records are from the Paleocene of the Indian Ocean and of the Volga basin, Russia. Twenty-six, perhaps twenty-seven, of its twenty-eight species have been found in Paleogene deposits. Six of these are also known from the Neogene, two of them, *R. hannai* R. Ross and *R. tenuicornis* Grunow, as different subspecies. Only one species, *R. szakalensis* Pantocsek, is known only from deposits which are certainly Neogene in age, but the material in which *R. flabellifera* R. Ross has been found may be either early Oligocene or early Miocene.

The sub-period from which the greatest number of species of *Rutilaria* has been recorded is the late Eocene, twelve species having been found in deposits that are certainly of this age, one of them, *R. areolata* Sheshukova-Poretskaya, represented by two subspecies. At least two, and probably four, further species occurred during this sub-period. *R. barbadensis* R. Ross and *R. elliptica* Greville are recorded from the middle Eocene and also from a deposit at about the Eocene to Oligocene boundary, so must have existed throughout the late Eocene. *R. interrupta* R. Ross has been found in a sample which may be middle Eocene or very early late Eocene in age, and it almost certainly survived into the later sub-period. Jousé (1979) identified a diatom from a sample of late Eocene age from the mid-Atlantic ridge as *R. philippinarum* Cleve & Grove, but her figure shows that this was a misidentification; the species she found and illustrated is probably *R. briggeri* R. Ross (see p. 37 above), otherwise known only from the middle Eocene.

The middle Eocene is the sub-period from which the next highest number of species of *Rutilaria* are known. There are certain records of eleven species from this, and a further species, *R. amplectans* (Grove & Sturt) R. Ross, is known from a sample from its upper boundary. In contrast, only two species are known from deposits that are certainly of early Eocene age, although some of the samples from the Fur formation of Denmark in which *R. minima* subsp. *danica* occurs may date from after the Paleocene to Eocene boundary. There are clearly phylogenetic connections between the five Paleocene species and species occurring in the middle Eocene. A number of intermediate species must therefore have been present during the lower Eocene, although the only one known from that period that may be such an intermediate is *R. kamyshlovensis* R. Ross.

Rutilaria philippinarum is one of the two species of *Rutilaria* known to be living today. It is known from the upper Eocene of Oamaru, New Zealand, and there are records of it throughout the Miocene, but none from the Oligocene or from the Pliocene, although it must have been present then. It is thus clear that the number of species known from any geological period is, at least in part, dependent on the availability of fossil deposits of that age and the extent to which they have been studied. Nine of the twelve species with certain records from the late Eocene have been found in the Oamaru diatomite, a deposit that has been studied more thoroughly than any other. Nevertheless, whilst it is not possible to attach any significance to changes in the number of taxa known to be present between one sub-period and the next, there were obviously many fewer species in the Pliocene than there were in the Eocene. However, what we know of the fossil record does not tell us whether this fall in numbers coincided with the Oligocene–Miocene boundary or was earlier or later.

The two living species of *Rutilaria*, *R. tenuicornis* and *R. philippinarum*, both occur in the neritic plankton. Most, if not all, of the fossil deposits in which members of the genus have been found seem to have been laid down in comparatively shallow water; they do not consist entirely of oceanic species. This suggests that the fossil species also were part of the neritic plankton and that the genus, in spite of its diversity, had a limited ecological range as far as habitat is concerned. The two living species occur only in tropical and subtropical waters of the western Pacific and Indian Oceans. Whilst it is quite possible that all the fossil species also occurred in warm waters, there is much more uncertainty about this. Too little is known about the temperature of the water from which some were deposited.
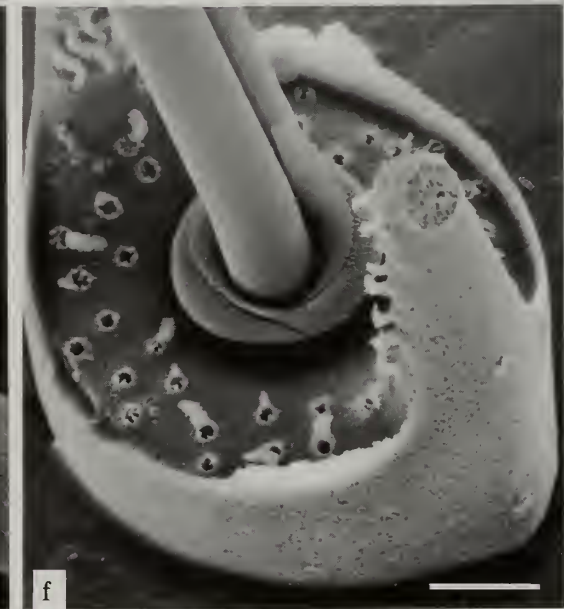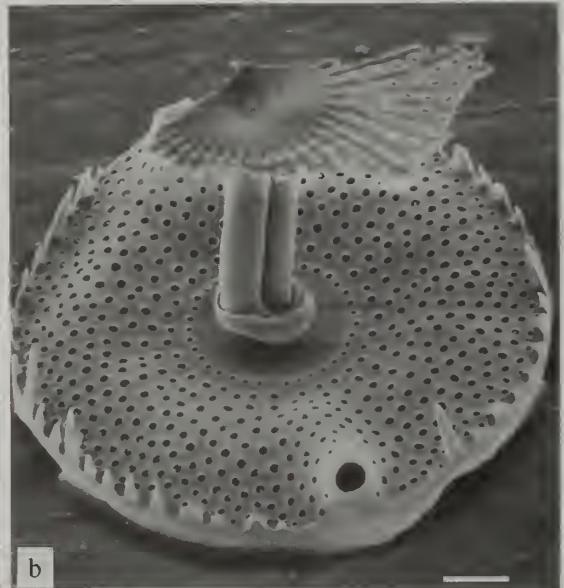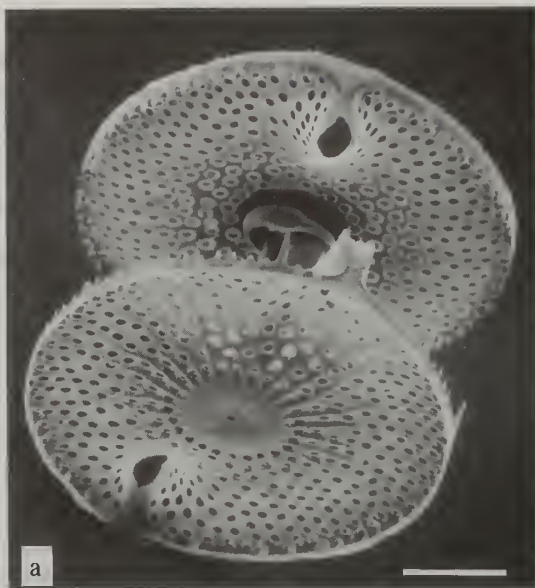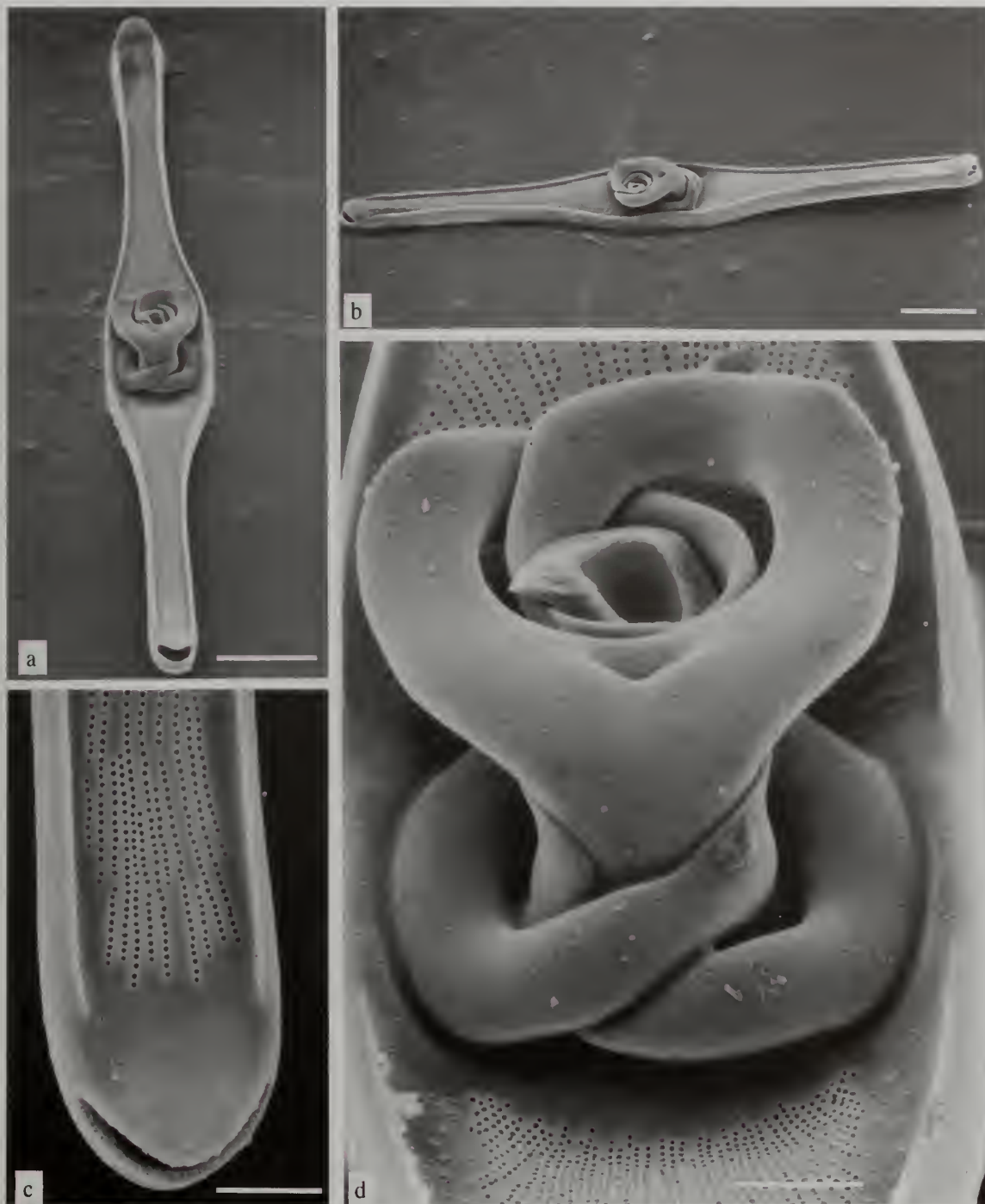
Plate II *Rutilaria interrupta*, Falkland Plateau, South-western Atlantic Ocean. (a): valve view of valve with sibling periplekton attached (SEM 35956); (b): oblique valve view of same specimen as (a) showing marginal ridge (SEM 35952); (c): detail of (a), apex of valve, ocellus broken away (SEM 35948); (d): detail of (a), sibling periplekta showing arms of ring encircling broken stem of sibling (SEM 35955). (a), (b), bar = 25 μm; (c), (d), bar = 5 μm.

Plate I (a)–(c): *Rutilaria grevilleana* subsp. *grevilleana*. (a): oblique view of two sibling valves, Mascarene Ridge, Indian Ocean (SEM 2420); (b): oblique view of valve with periplekton and fragment of sibling valve attached, internal opening of periplekton visible on valve fragment, plate of ocellus broken away, Joe's River, Barbados (SEM 85042); (c): girdle view of two sibling valves showing periplekta, Joe's River, Barbados (SEM 72208). (a)–(c), bar = 10 μm. (d)–(f): *Rutilaria amplectans*. (d): girdle view of two sibling valves, showing periplekta and tall elevations with superficial spines, Oamaru, New Zealand (SEM 72671); (e): detail of (d), upper parts of sibling periplekta showing arms of ring surrounding stem of sibling, Oamaru, New Zealand (SEM 72675); (f): oblique valve view showing ocellus with porelli on elevation and stem and ring of sibling periplekton, Division Hill, Oamaru, New Zealand (SEM 103155). (d), bar = 20 μm; (e)–(f), bar = 5 μm.
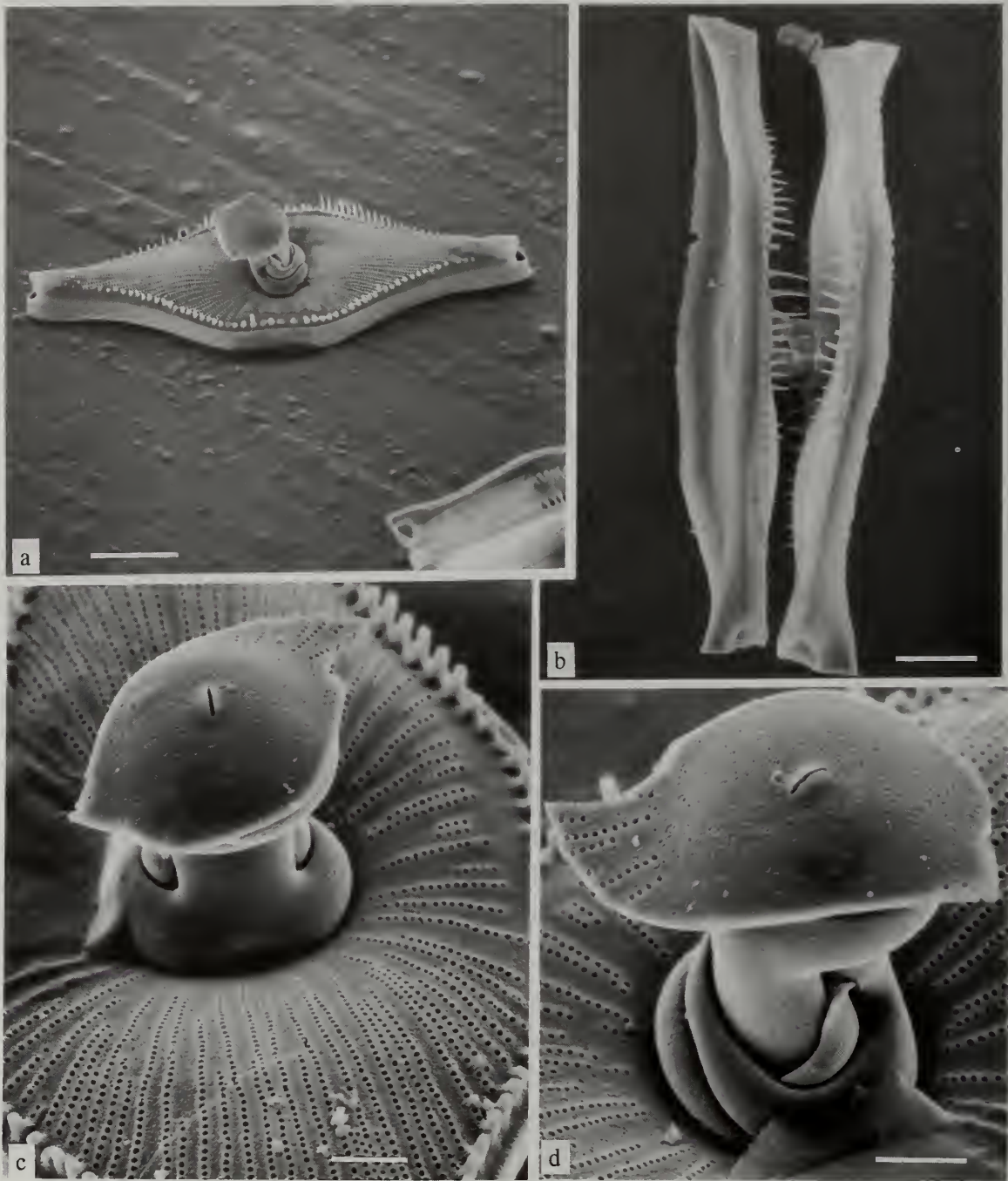
Plate III *Rutilaria radiata*, Oamaru, New Zealand. (a): valve view with periplekton and fragment of sibling valve attached (SEM 72775); (b): girdle view of pair of sibling valves (SEM 72768); (c): same specimen as (a), sibling periplekta showing ring and internal opening (SEM 2747); (d): periplekta of same specimen viewed from other side (SEM 2748). (a), bar = 20 μm; (b), bar = 10 μm; (c), (d), bar = 5 μm.

Plate IV *Rutilaria hannai* subsp. *hannai*, Cantua Creek, Fresno County, California, U.S.A.. (a): valve view of whole frustule (SEM 97987); (b): girdle view of frustule and attached valve (SEM 97996); (c): same specimen as (a), apex of valve showing ocellus with porelli and girdle bands (SEM 112975); (d): detail of (b), apical part of valves showing ocelli with porelli and girdle bands (SEM 98048); (e): oblique view of pair of sibling valves (SEM 112977); (f): detail of (e), central portion showing marginal spines and internal opening of periplekton (SEM 112978). (a), (b), (e), bar = 20 μm; (c), (d), (f), bar = 5 μm.
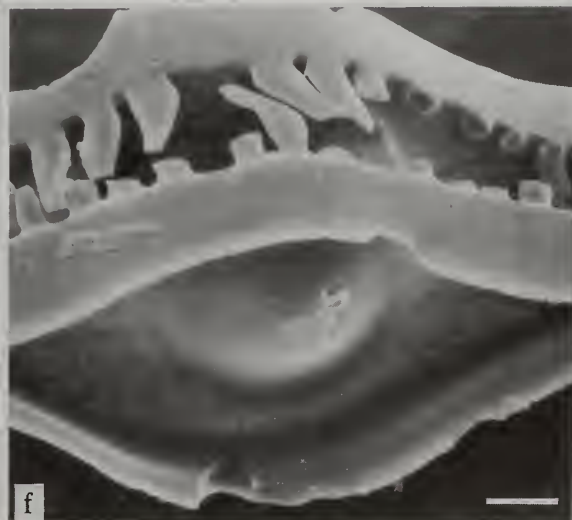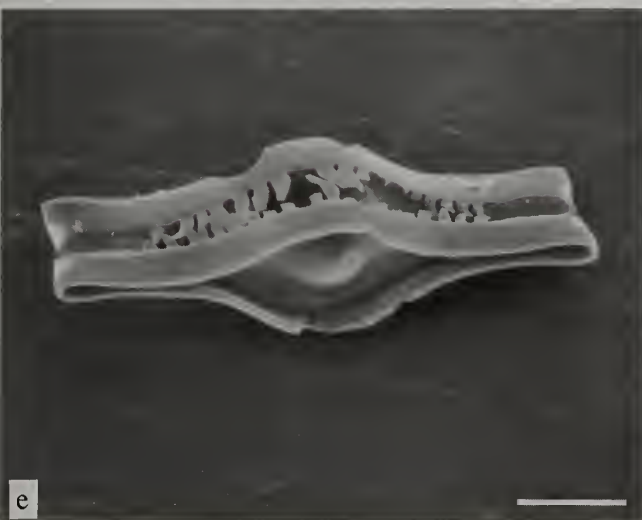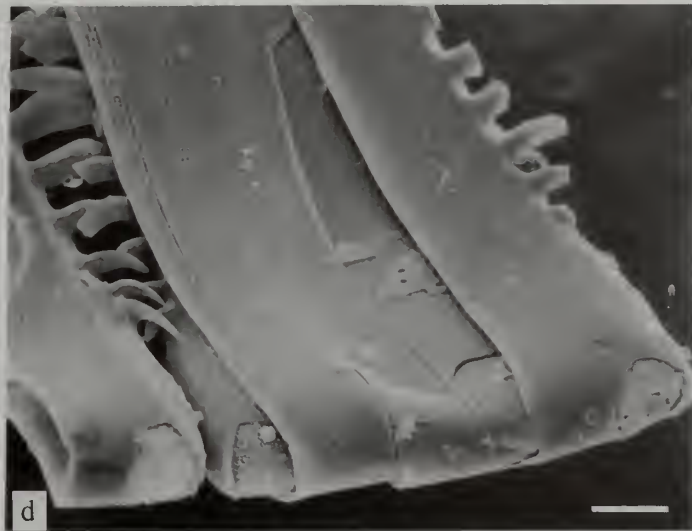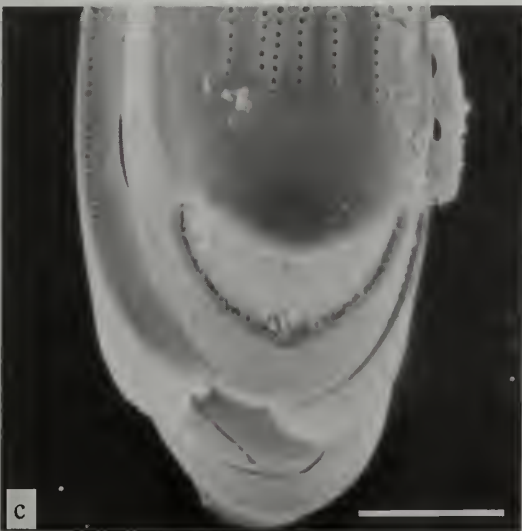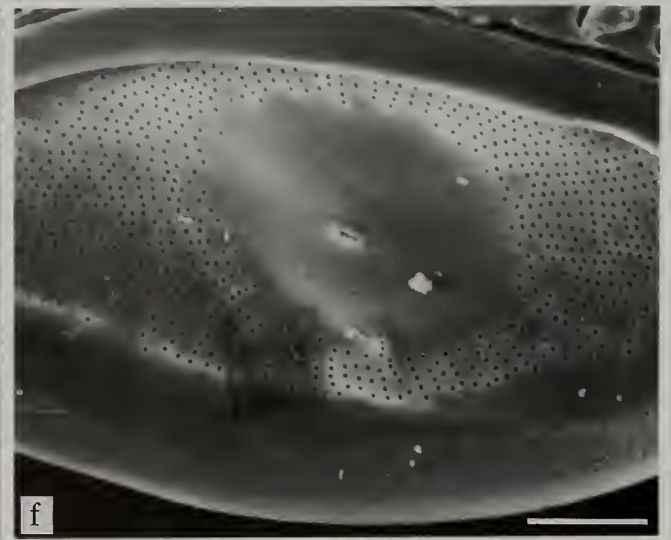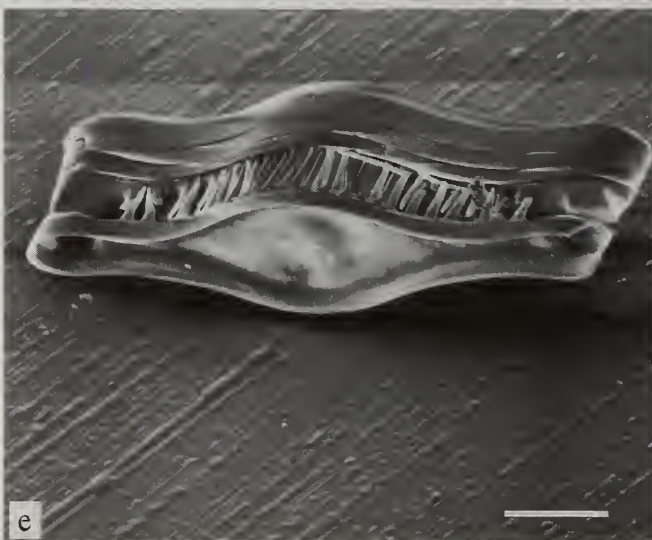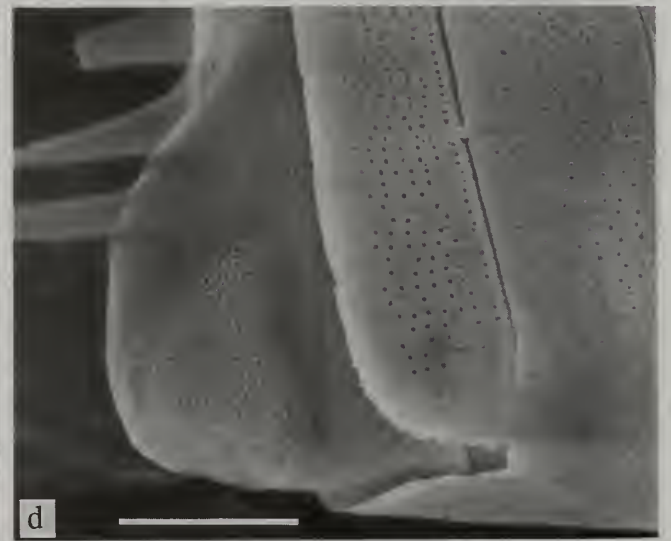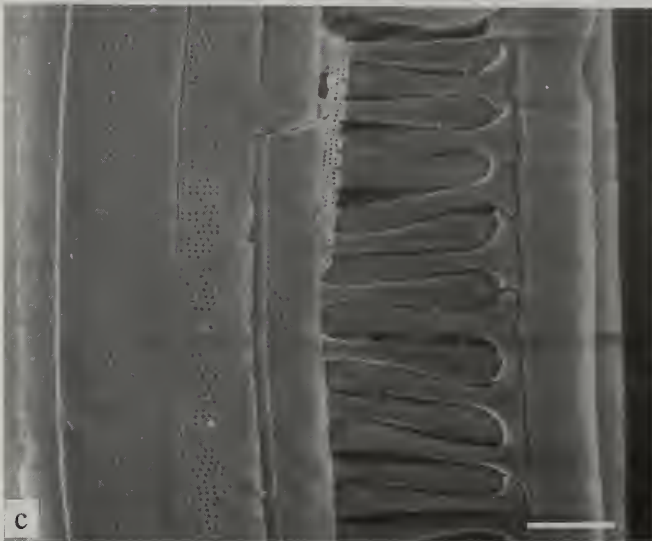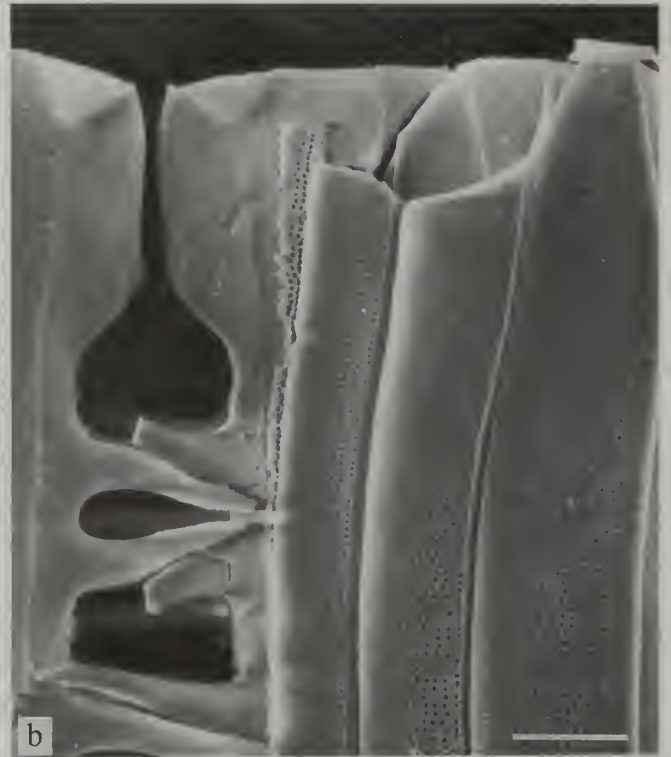
Plate VI *Rutilaria minima* subsp. *minima*, Inza, Ulyanovsk oblast, Russia. (a): valve view of frustule showing marginal costa and costa inset from margin (SEM 113320); (b): same specimen as (a), oblique view (SEM 113324); (c): detail of (a), apex of valve with girdle bands and ocellus with porelli (SEM 113321); (d): detail of (a), centre of valve with broken periplekton (SEM 113322). (a), (b), bar = 10 μm; (c), (d), bar = 2 μm.

Plate V *Rutilaria kamyshlovensis*, 'Kamichev', Russia. (a): girdle view of pair of sibling valves, one with girdle of missing epivalve attached (SEM 59928); (b): detail of (a) showing apical elevation and girdle bands (SEM 112967); (c): detail of (a), central part showing interlocking marginal spines with small basal tubercles, and girdle bands (SEM 59933); (d): apex of valve showing ocellus with porelli (SEM 72201); (e): same specimen as (a), oblique view (SEM 112971); (f): detail of (e), central portion of valve showing internal opening of periplekton and interlocking linking spines with small basal tubercles (SEM 112972). (a), (e), bar = 20 μm; (b)–(d), (f), bar = 5 μm.
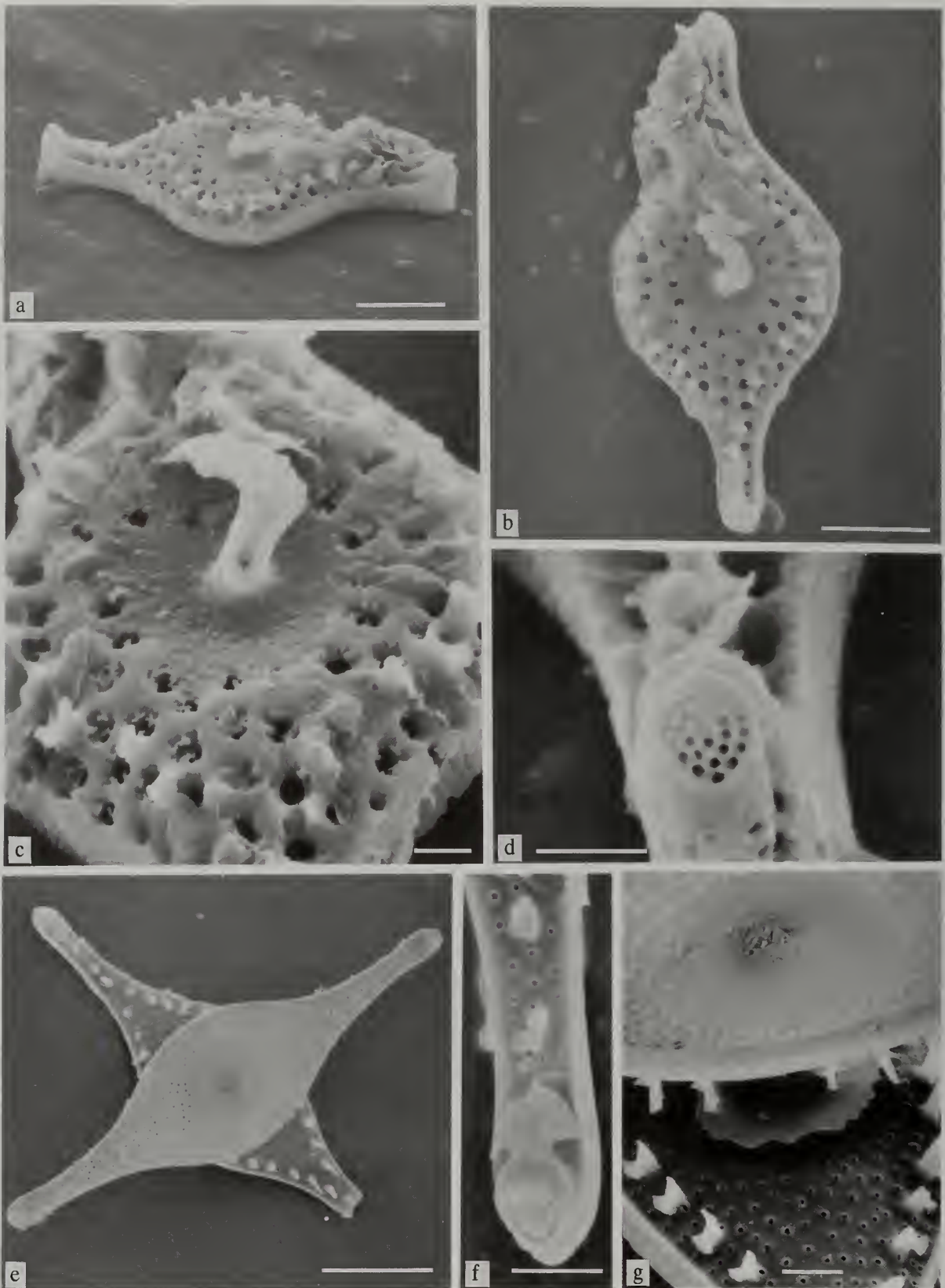
Plate VII (a)–(d): *Rutilaria areolata* subsp. *areolata*, Labrador Sea, North Atlantic Ocean. (a): oblique valve view of single valve, (SEM 70357); (b): valve view of same specimen as (a) (SEM 70348); (c): detail of (b), central portion with broken periplekton and tubercles on marginal spines (SEM 70352); (d): detail of (b), apex of valve showing ocellus with protruding upper margin and winged costa, somewhat obscured by dirt, attached to elevation (SEM 70351). (a), (b), bar = 5 μm; (c), (d), bar = 1 μm. (e)–(g): *Rutilaria areolata* subsp. *tenuior*, Barbados. (e): valve view of sibling pair (SEM 72280); (f)::detail of (e), apex of valve showing ocellus with protrusions on upper margin and winged costa attached to proximal side of elevation (SEM 72281); (g): detail of (e), centres of valves, edge of flange of periplekton and internal opening (SEM 72284). (e), bar = 10 μm; (f), (g), bar = 2 μm.
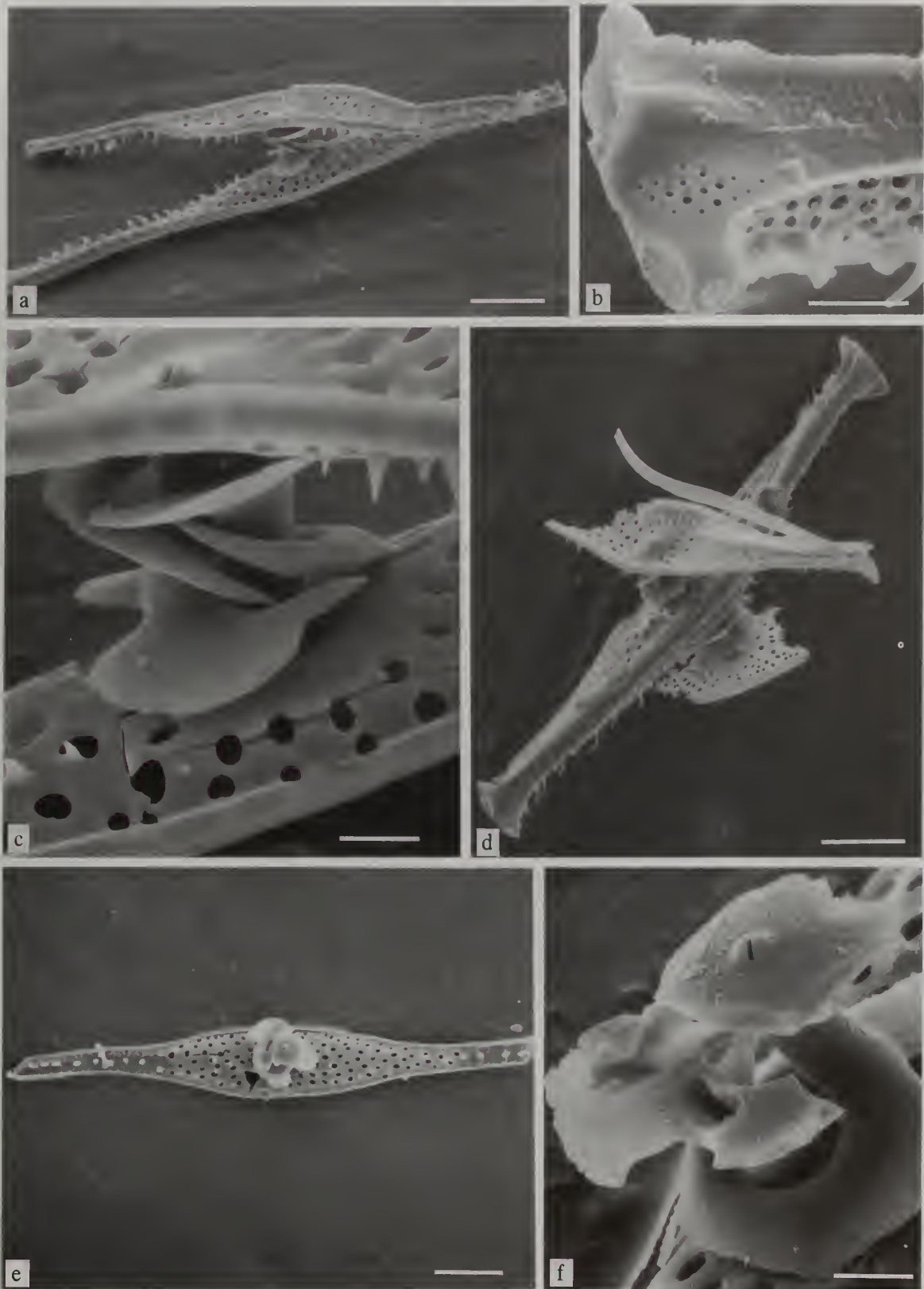
Plate VIII *Rutilaria schenkii*, Cantua Creek, Fresno County, California, U.S.A. (a): oblique view of sibling pair of valves (SEM 97982); (b): detail of (d), apex of frustule showing ocellus with porelli, poroids on mantle near apex and costa on proximal side of elevation (SEM 98051); (c): detail of (a) showing periplekta with flange and interlocking tips of longer arms (SEM 97981); (d): oblique view of frustule with parts of sibling valves attached (SEM 97978); (e): valve view of valve with sibling periplekton attached, both periplekta with arms broken and flange eroded (SEM 97983); (f): detail of (e) showing periplekta of two sibling valves with arms broken and flange eroded (SEM 98047). (a), (d), (e), bar = 10 μm; (b), (c), (f), bar = 2 μm.
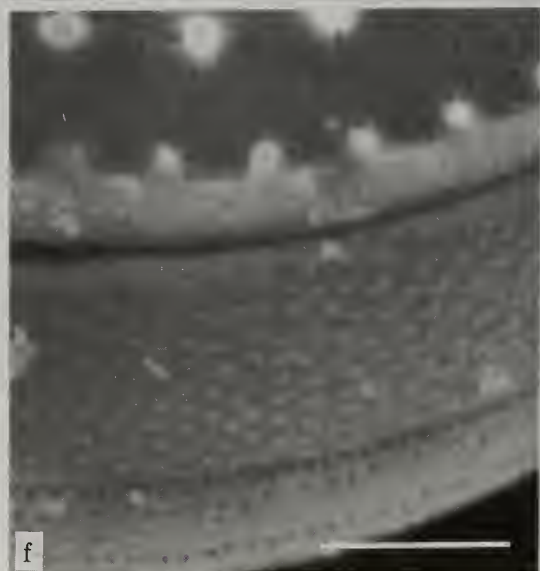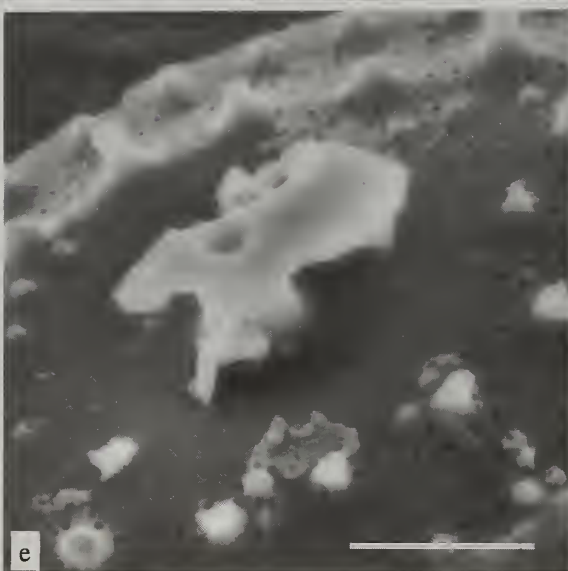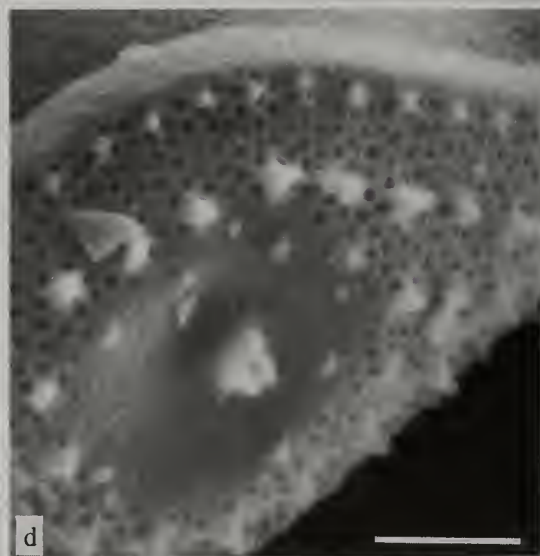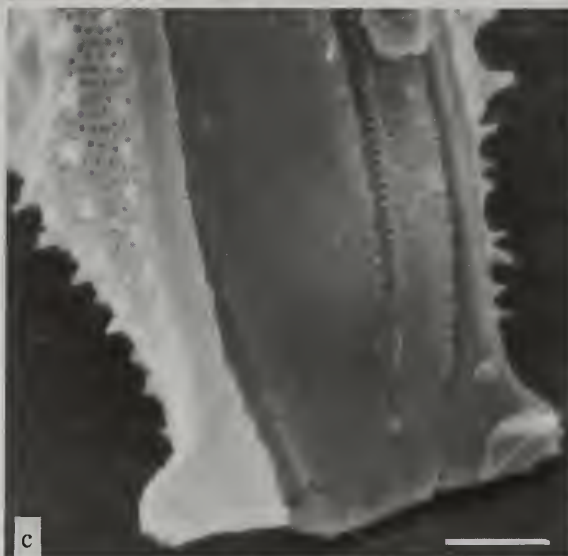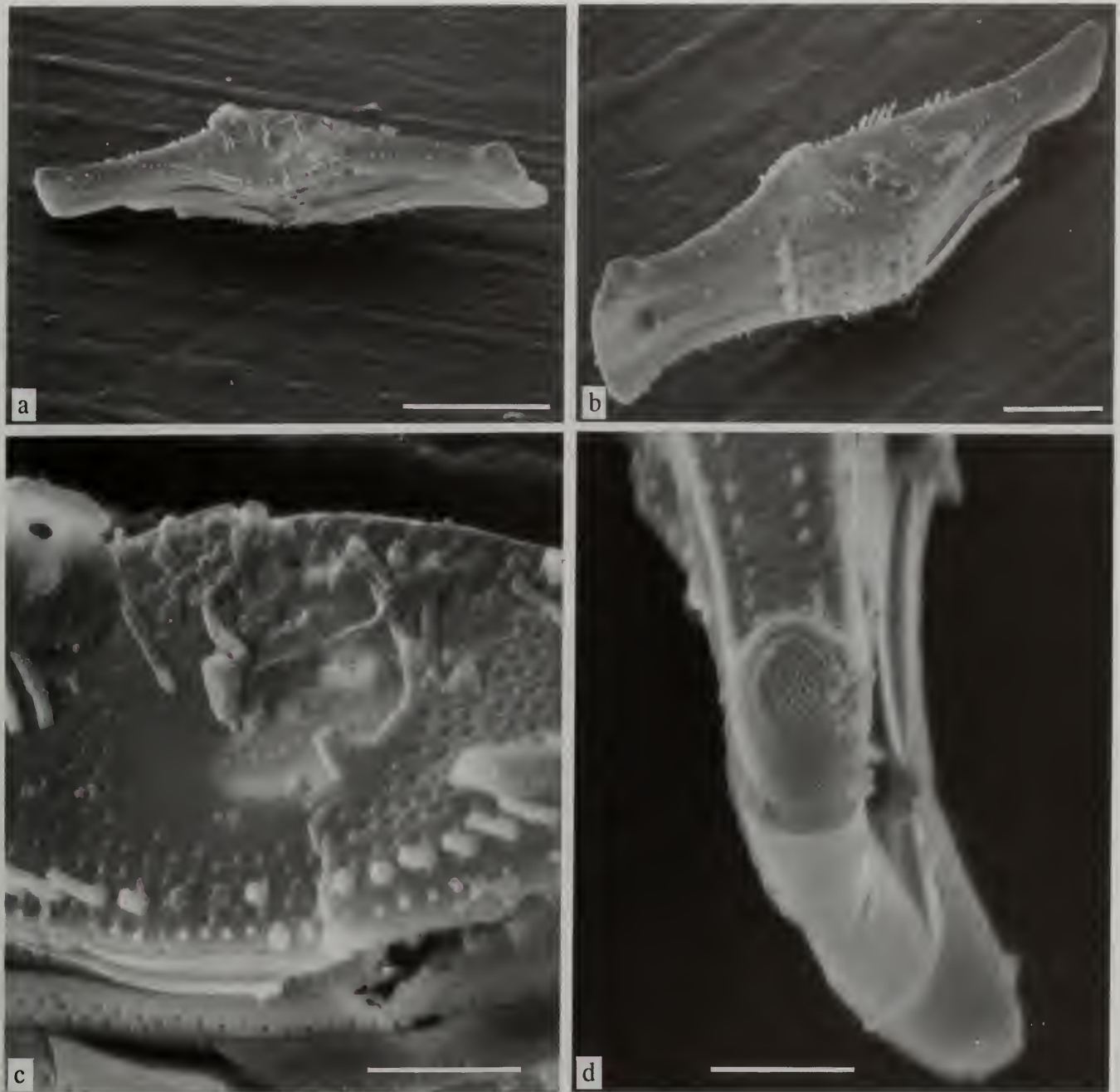
Plate X *Rutilaria hyalina*, Inza, Ulyanovsk oblast, Russia. (a): oblique valve view of frustule (SEM 113308); (b): oblique valve view of another frustule (SEM 113312); (c): detail of (a), centre of valve with inner row of cylindrical marginal spines and outer row of minute marginal spines (SEM 113309); (d): same specimen as (b), apex with elevation and ocellus with porelli (SEM 113311). (a), bar = 10 μm; (b), bar = 5 μm; (c), (d), bar = 2 μm.

Plate IX *Rutilaria delicatula*, Inza, Ulyanovsk oblast, Russia. (a): oblique valve view of frustule showing marginal spines in two rows (SEM 113300); (b): detail of (a), apex of valve showing elevation and ocellus with porelli (SEM 113301); (c): apex of frustule in girdle view showing elevations and girdle bands, also fasciculate arrangement of areolae (SEM 113319); (d): oblique view of centre of valve showing broken periplekton and marginal spines in two rows and fasciculate arrangement of areolae (SEM 113316); (e): oblique view of centre of another valve with periplekton, part of the ring broken away (SEM 113307); (f): oblique view of central part of same specimen as (a) showing verrucose girdle band (SEM 113303). (a), bar = 5 μm; (b)–(f), bar = 2 μm.
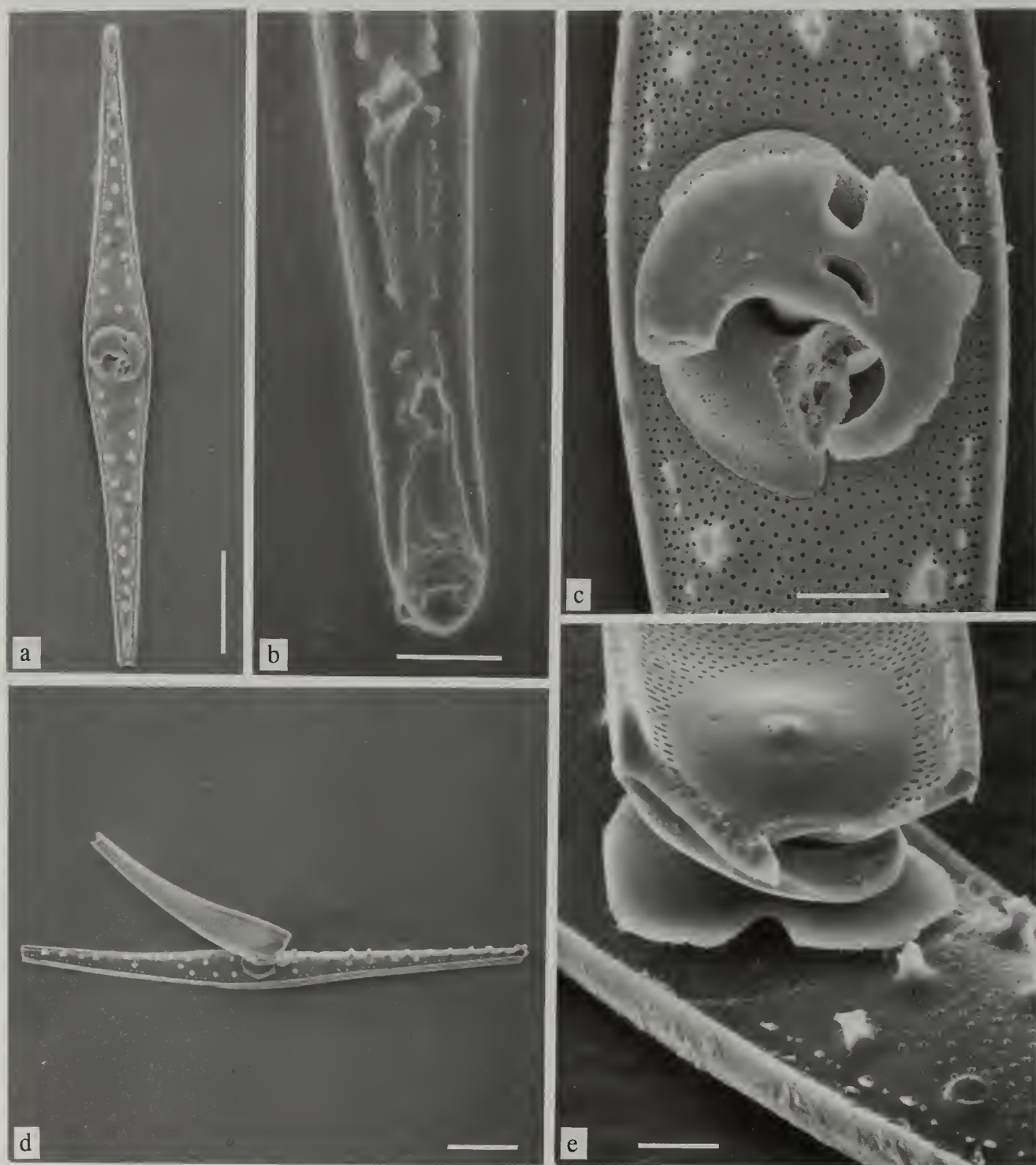
Plate XI *Rutilaria briggeri*, Bermuda Rise, North Atlantic Ocean. (a): valve view of valve with sibling periplekton attached (SEM 72250); (b): detail of (a), distal part of valve with marginal spines of outer rows united to form costae (SEM 72258); (c): detail of (a) showing periplekton with longer arm broken and ring of sibling periplekton broken off stem (SEM 72251); (d): oblique view of valve with part of sibling valve attached (SEM 113296); (e): detail of (d): central part of sibling pair with the upper valve broken at the edge of the central area and periplekta visible (SEM 15586). (a), (d), bar = 20 μm; (b), (c), (e), bar = 3 μm.
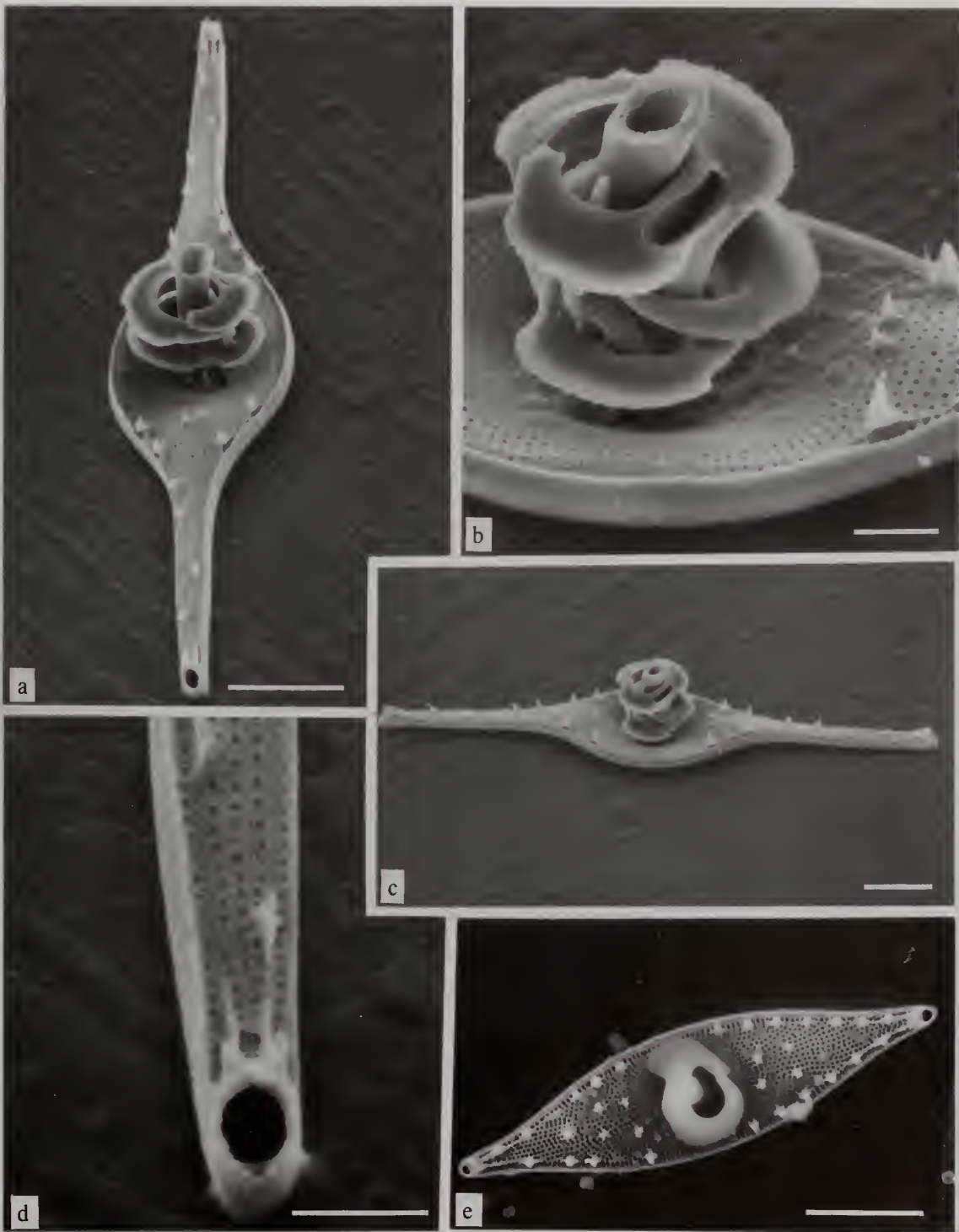
Plate XII (a)–(d): *Rutilaria tenuicornis* subsp. *tenuicornis*, Road from Mantoep to Pelang, Java. (a): oblique valve view of valve with sibling periplekton attached (SEM 70103); (b): detail of (c) showing periplekta with flange with gap and with tips of longer arms deflected towards the valve from which they arise (SEM 70108); (c): same specimen as (a), oblique valve view (SEM 70109); (d) detail of (a) showing distal part of valve with short costae attached to elevations and costate extensions of distal marginal spines (SEM 70107). (a), (c), bar = 10 μm, (b), (d), bar = 3 μm. (e) *Rutilaria tenuicornis* subsp. *paleogena*, valve view, Dneiper–Dombas depression, Ukraine, (SEM by A. Olshtynskaya). Bar = 10 μm.
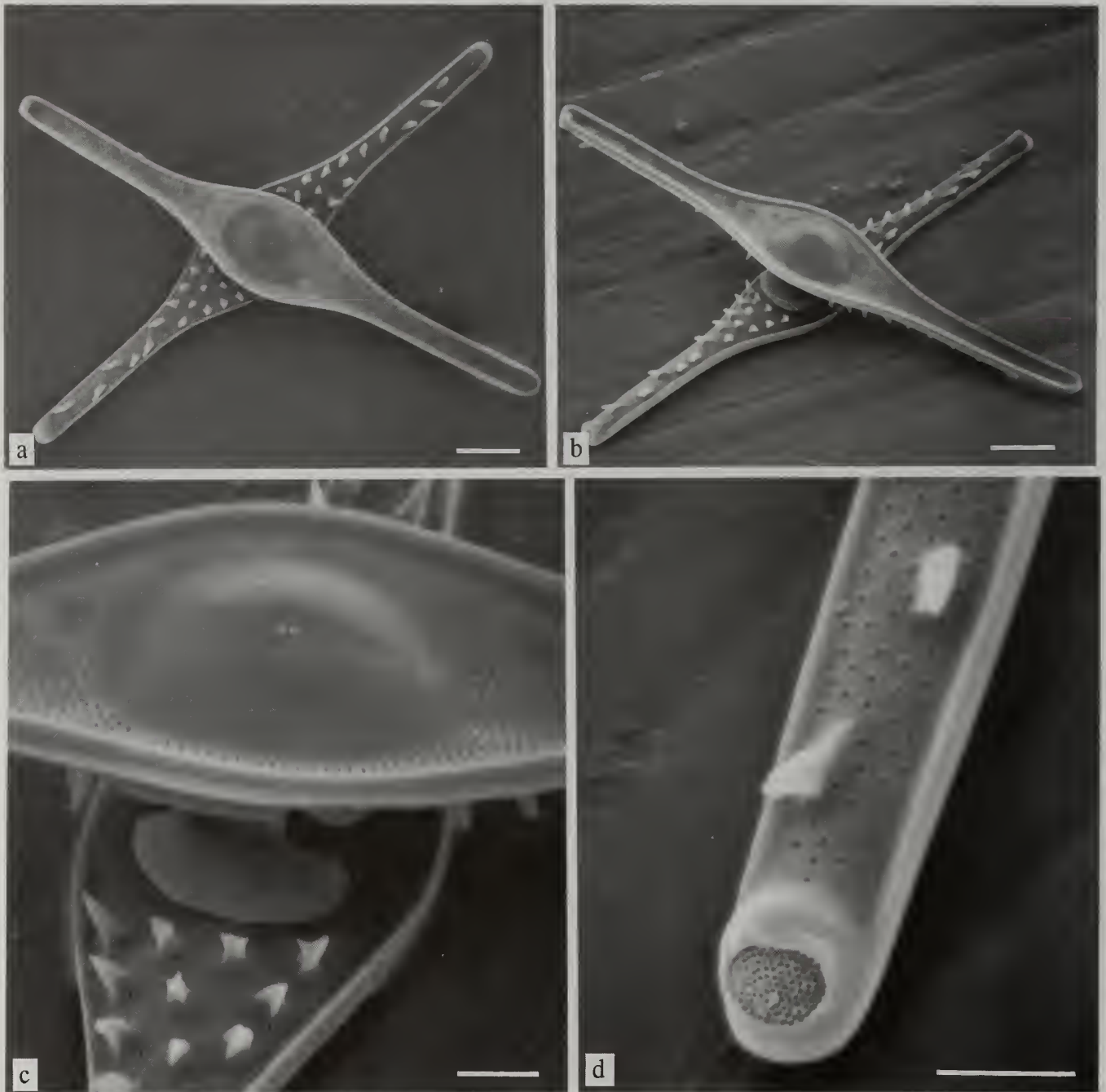
Plate XIII *Rutilaria tenuis*, Falkland Plateau, south-western Atlantic Ocean, 51° 08′ S, 54° 22′ W, Vema cruise 17, core 107, 50 cm. (a): valve view of sibling pair of valves lying at an angle (SEM 113341); (b): oblique view of same specimen as (a) (SEM 113344); (c): same specimen, oblique view of central part of valve showing internal opening of periplekton and flanged ring with gap in flange (SEM 113348); (d): detail of (a), apex of valve with marginal spines and elevation with ocellus with porelli (SEM 113346). (a), (b), bar = 10 μm; (c), (d), bar = 3 μm.
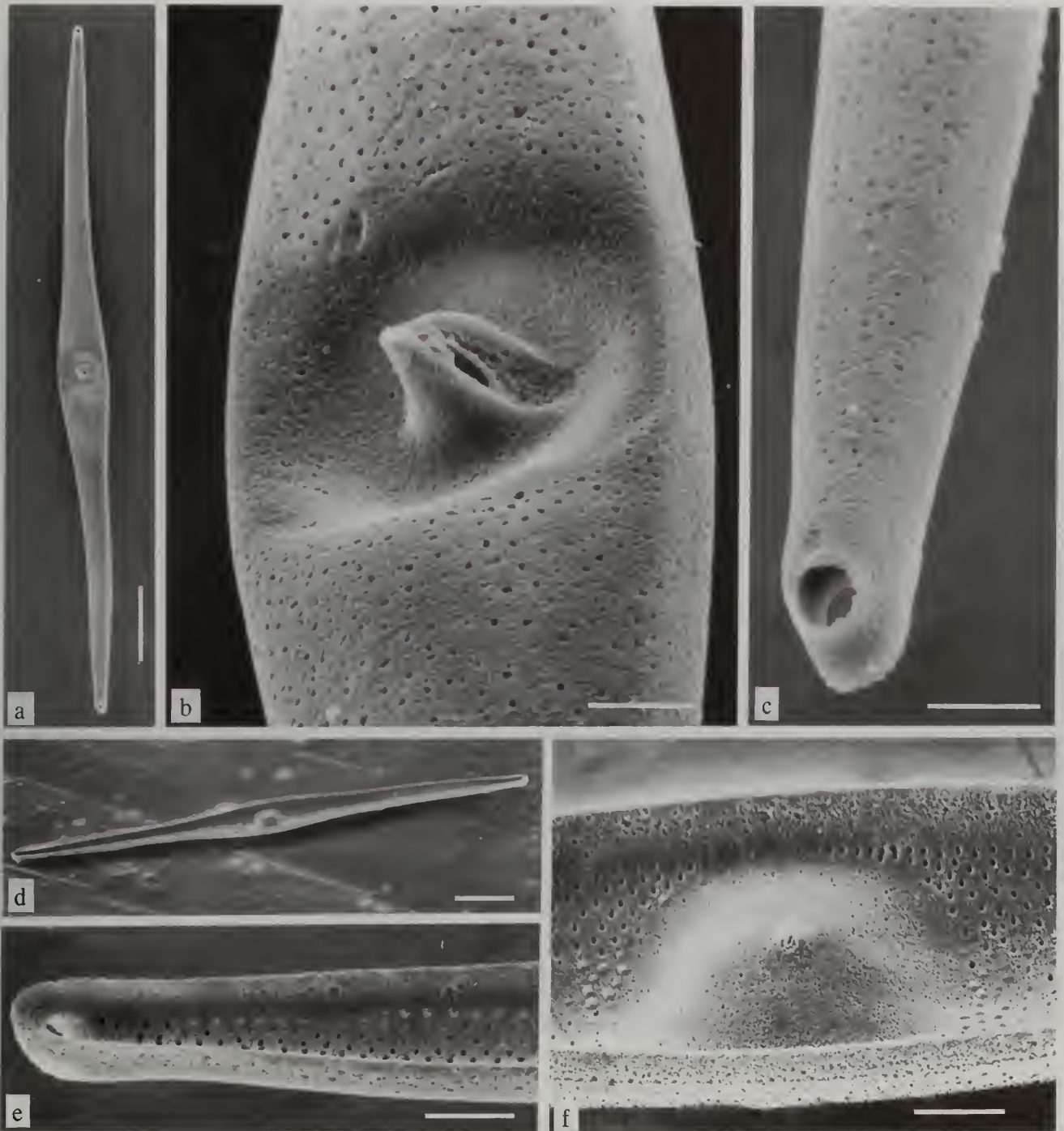
Plate XIV　*Rutilaria lanceolata*, Oamaru, New Zealand. (a): valve view of valve with periplekton broken off (SEM 72690); (b): detail of (a) showing central portion of valve with depressed central area (SEM 72688); (c): detail of (a), distal part of valve showing ocellus broken away, longitudinal striae and valve curving down into hyaline mantle (SEM 72689); (d): oblique internal valve view of single valve (SEM 72816); (e): detail of (d) showing apex of valve (SEM 72818); (f): detail of (d) showing centre of valve with internal opening of periplekton (SEM 72817). (a), (d), bar = 20 μm; (b), (c), (e), (f), bar = 3 μm.
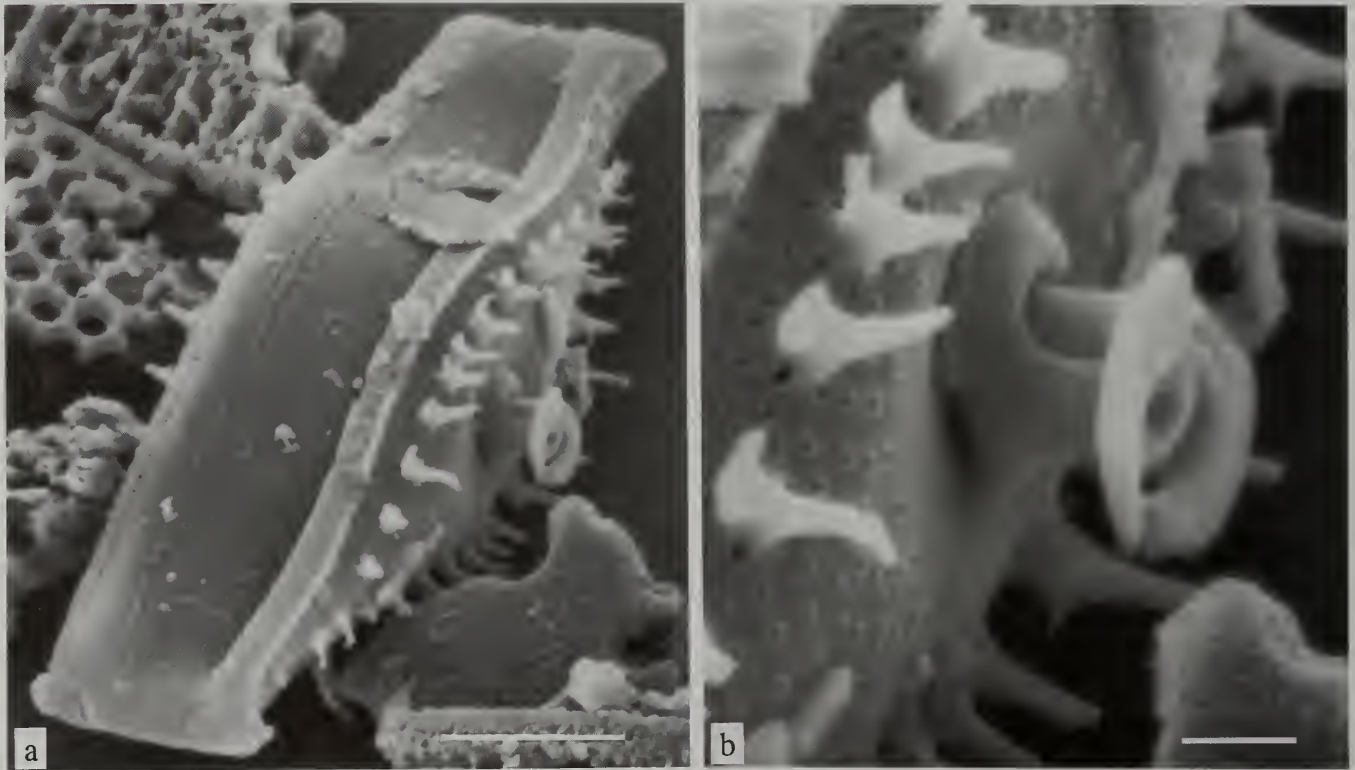
Plate XV *Rutilaria hustedtii*, Inza, Ulyanovsk oblast, Russia. (a): oblique girdle view of frustule (SEM 113362); (b): detail of (a) showing tubercles on outer side of marginal spines and periplekton with narrow flange with gap (SEM 113361). (a), bar = 5 μm; (b), bar = 1 μm.
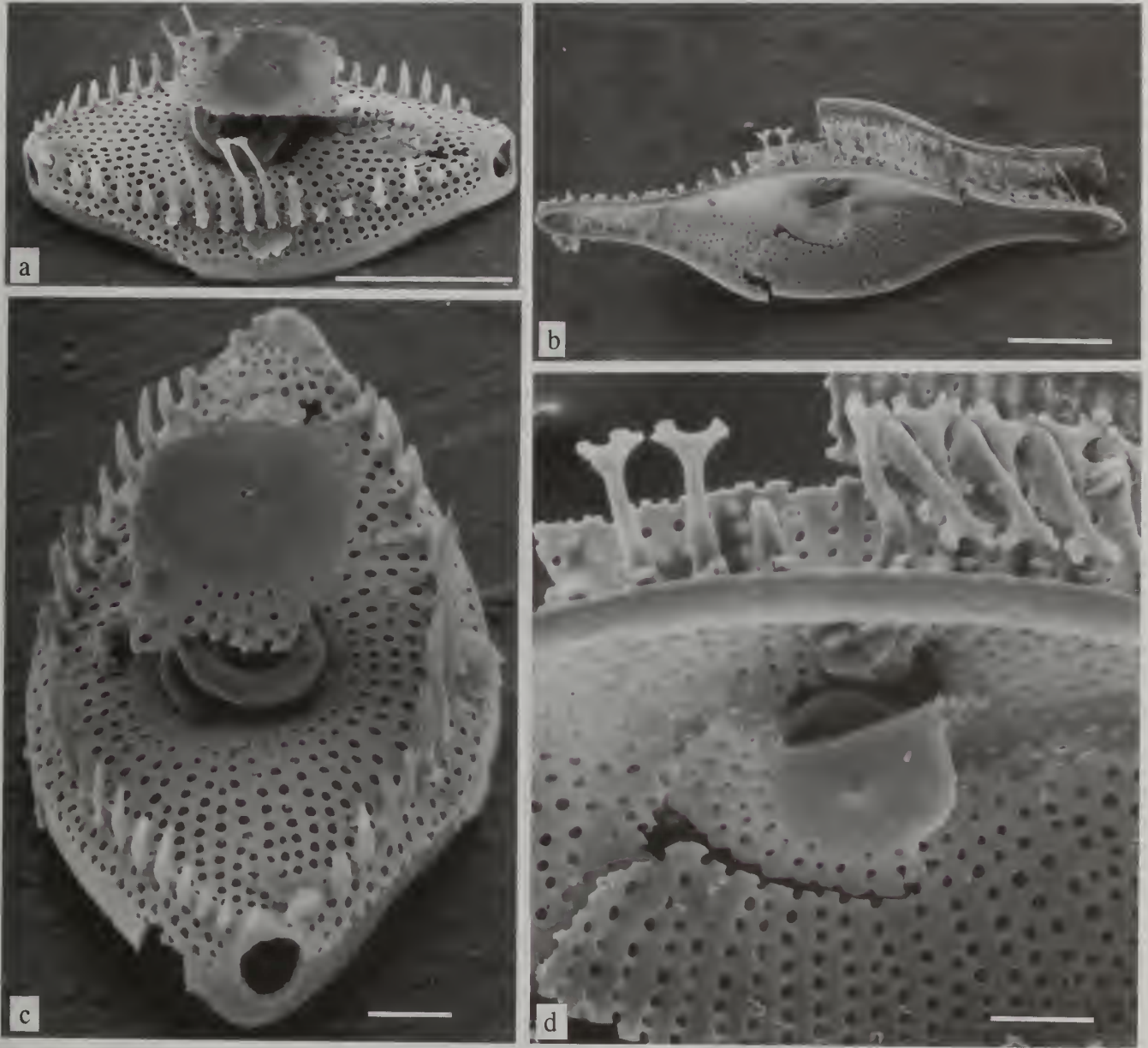
Plate XVI *Rutilaria elliptica*, Barbados. (a): oblique valve view with periplekton and fragment of sibling valve attached, showing tubercles at base of marginal spines and expanded tips to central marginal spines (SEM 72274); (b): oblique girdle view of valve and half of sibling valve (SEM 104732); (c): same specimen as (a), oblique valve view, ocellus broken away (SEM 72276); (d): detail of (b) showing interlocking linking spines and internal opening of periplekton (SEM 104733). (a), (b), bar = 20 μm; (c), (d), bar = 5 μm.

Plate XVII *Rutilaria philippinarum*, Paradise Beach, Malibu, Los Angeles County, California, U.S.A. (a): oblique valve view of valve with sibling periplekton attached (SEM 71393); (b): detail of (a), central part showing periplekton, interlocking marginal spines with basal tubercles, and superficial spines (SEM 71394); (c): girdle view of chain of two frustules with two attached valves (SEM CB09.504); (d): oblique girdle view of a pair of sibling valves (SEM 36527); (e): same specimen as (d), centres of valves showing interlocking marginal spines with tubercles at base (SEM 36525); (f): same specimen as (d), apices of valves showing ocelli with porelli (SEM 36524). (a), (c), (d), bar = 20 μm; (b), (e), bar = 5 μm; (f), bar = 2 μm.

Plate XVIII *Rutilaria szakalensis*, 'Castel', Szurdokpüspöki, Hungary. (a): oblique valve view of hypovalve and girdle of epivalve of same frustule with periplekton of sibling valve attached (SEM 70403); (b): same specimen as (a), periplekta, one with shorter arm broken (SEM 70408); (c): same specimen as (a), apex showing elevation, ocellus and ligula of copula III (SEM 70409); (d): detail of (a), other apex of same specimen as (c) showing ligula of copula II (SEM 70402); (e): girdle view of two frustules, one young and with no hypocingulum, the other with epivalve lost, (SEM 70412); (f): detail of (e) showing ocelli with porelli, terminal elevations, and interlinked marginal spines with very small tubercles a little above their bases (SEM 70413). (a), (e), bar = 10 μm; (b)–(d), (f), bar = 3 μm.

Plate XIX *Rutilaria epsilon*. (a): oblique valve view of valve with attached sibling periplekton, showing flange on ring of periplekton, Malibu, Los Angeles County, California, U.S.A. (SEM 97817); (b): oblique valve view of central part of valve with attached sibling periplekton, showing marginal spines with tubercles and dendroid superficial spines, Sendai, Miyagi Prefecture, Honshu, Japan (SEM 73346); (c): same specimen as (b), valve view of central part of the valve with periplekta (SEM 73341); (d): detail of (a), apex of valve with ocellus with porelli and protrusions on its upper margin (SEM 97820); (e): girdle view of a chain of three frustules and two attached valves, Sendai, Miyagi Prefecture, Honshu, Japan, (SEM 66197); (f): detail of (e) showing girdle bands (SEM 66198). (a), (e), bar = 20 μm; (b), (c), (f), bar = 5 μm; (d), bar = 1 μm.
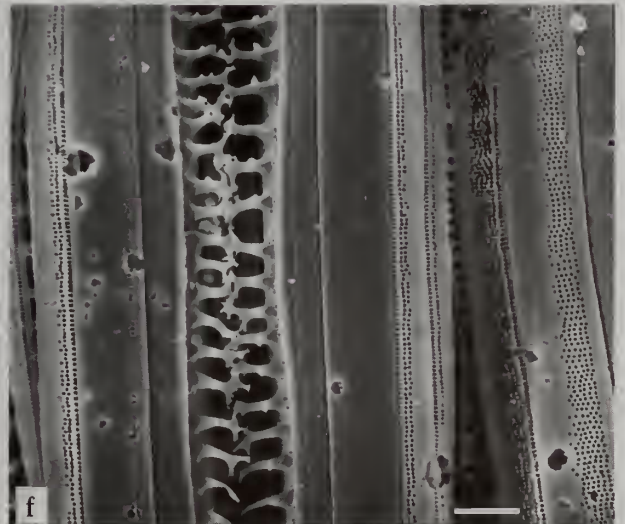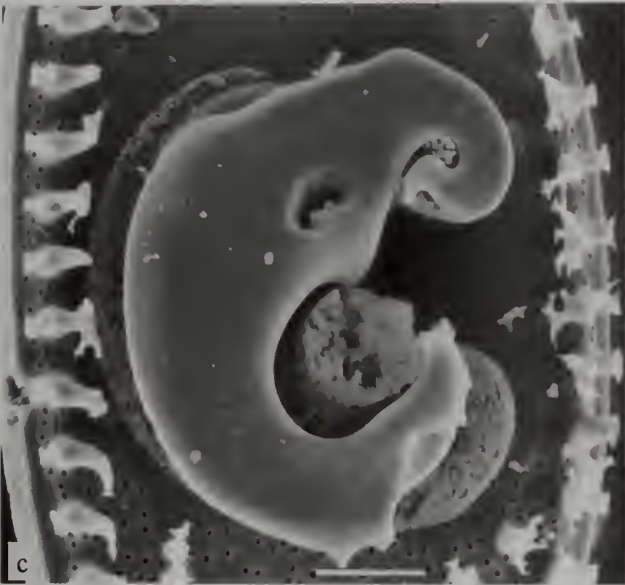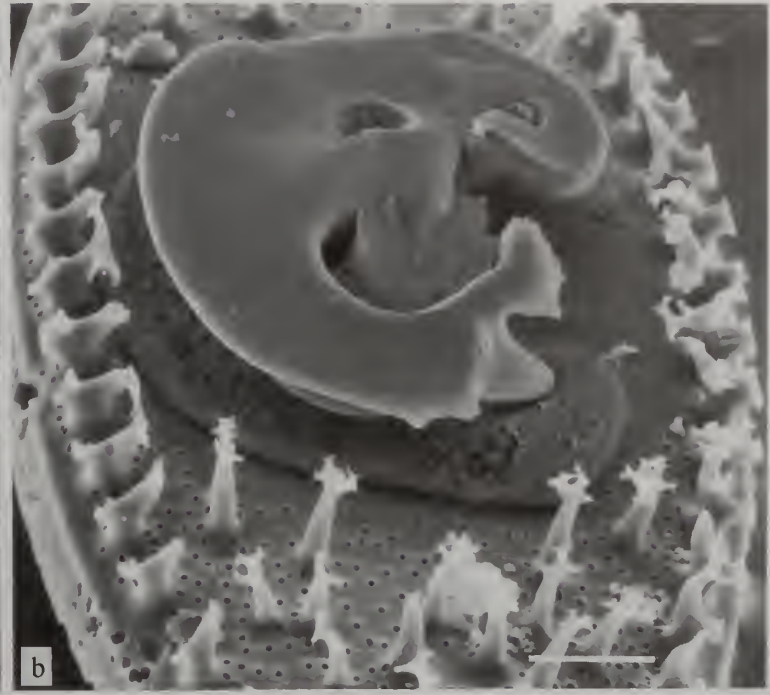
Plate XX *Rutilaria obesa*, (a): oblique valve view of valve with periplekton and fragment of sibling valve attached, Hakodate, Oshima, Hokkaido, Japan (SEM 73355); (b): oblique valve view of central portion of similar specimen to (a) showing flange on ring of periplekton, knob on end of shorter arm and end of longer arm deflected back towards valve from which it arises, Hakodate, Oshima, Hokkaido, Japan (SEM 73352); (c): oblique view of valve and central part of sibling valve, Temescal Canyon, Santa Monica, Los Angeles County, California, U.S.A. (SEM 112431); (d): oblique valve view of centre of valve with attached sibling periplekton showing flange on ring, knob on end of shorter arm of ring and end of longer arm of ring deflected back towards valve from which it arises, Palos Verdes, Los Angeles County, U.S.A. (SEM B3/424); (e): oblique girdle view of chain of frustules showing marginal spines expanded above and abutting, Temescal Canyon, Santa Monica, Los Angeles County, California, U.S.A. (SEM 112438): (f): same specimen as (e), apical part showing ocelli, ligulae and areolae on girdle bands (SEM 80763). (a), bar = 20 μm; (b), (c), (e), bar = 10 μm; (d), (f), bar = 3 μm.

REFERENCES

Akiba, F. 1985. Middle Miocene to Quaternary diatom biostratigraphy in the Nankai Trough and Japan Trench, and modified lower Miocene through Quaternary diatom zones for middle-to-high latitudes of the north Pacific. *Initial Rep. deep Sea Drilling Proj.* 87: 393–481.
—— 1987. Neogene diatom biostratigraphy of the Nakayama-Toge section, Sado Island, Japan, and its relation to the Funakawa floral change plane of

Yamanoi (1978). *Bull. Sado Museum* 9: 85–101. [In Japanese with English abstract].
—— & Yanagisawa, Y. 1985. Taxonomy, morphology and phylogeny of the Neogene diatom zonal marker species in the middle-to-high latitudes of the north Pacific. *Initial Rep. deep Sea Drilling Proj.* 87: 483–554.
Anonymous. 1975. Proposals for a standardization of diatom terminology and diagnoses. *Beih. nov. Hedwigia* 53: 323–354.
Baldauf, J.G. & Barron, J.A. 1987. Oligocene marine diatoms recovered in dredge samples from the Navarin Basin Province, Bering Sea. *Bull. U.S. Geol. Surv.* 1765: 1–17, pl. 1–4.
Barron, J.A. 1975. Late Miocene–early Pliocene marine diatoms from southern California. *Palaeontographica* 151B: 97–170, Taf. 12–26.
—— 1976a. Marine diatom and silicoflagellate biostratigraphy of the type Delmontian Stage and the type *Bolivina obliqua* Zone, California. *J. Res. U.S. geol. Surv.* 4: 339–351.
—— 1976b. Revised Miocene and Pliocene diatom biostratigraphy of Upper Newport Bay, Newport Beach, California. *Mar. Micropaleont.* 1: 27–63.
—— & Baldauf, J.G. 1986. Diatom stratigraphy of the lower Pliocene part of the Sisquoc Formation, Harris Grade section, California. *Micropaleontology* 32: 357–371.
—— & Mahood, A.D. 1993. Exceptionally well-preserved early Oligocene diatoms from glacial sediments of Prydz Bay, East Antarctica. *Micropaleontology* 39: 29–35.
Berggren, W.A. 1969. Cenozoic foraminiferal faunas. *Initial Rep. deep Sea Drilling Proj.* 1: 594–607.
Brun, J. 1894. Espèces nouvelles. *Diatomiste* 2: 86–88, pl. V–VI.
—— 1896. Diatomées Miocènes. Description des espèces. *Diatomiste* 2: 229–247, pl. XIX–XXIV.
—— & Tempère, J. 1889. Diatomées fossiles du Japon. *Mém. Soc. Phys. Hist. nat. Genève.* 30(9): 1–75, pl. I–IX [VIII].
Castracane, A.F. 1886. Report on the diatomaceae collected by H.M.S. Challenger during the years 1873–76. *Rep. scient. Results Voy. Challenger* (Bot.) 2.
Chenevière, E. 1933. A Szurdokpüspöki-i Kastély alatt levő új felsömiocén lelőhely diatomai. (Note sur la dépôt de terre à diatomées fossiles (Miocéne supérieur) récemment découvert prés de Szurdokpüspöki.) *Földt. Közl.* 63: 216–218.
—— 1934a. Note sur le dépôt de terre à diatomées fossiles (Miocéne supérieur) récemment découvert près de Szurdokpüspöki. *Bull. Soc. fr. Microsc.* 3: 33–36, pl. 3–4.
—— 1934b. Sur un dépôt fossile marin à diatomées situé à Kamischev (Russie centrale). *Bull. Soc. fr. Microsc.* 3: 103–107, pl. 5–8.
Clark, B.L. & Campbell, A.S. 1942. Eocene radiolarian faunas from the Mount Diablo area, California. *Spec. Pap. geol. Soc. Am.* 399: 1–112.
Cleve, P.T. 1901. Plankton from the Indian Ocean and the Malay Archipelago. *K. svenska VetenskAkad. Handl.* Ny Földj. 35(5): 1–58, pl. I–VIII.
—— & Grove, E. 1891. Sur quelques diatomées nouvelles ou peu connues. *Diatomiste* 1: 64–68, pl. 10.
Coombs, L.D. 1952. Biddulphia dissipata–Syndetoneis amplectans. *Microscope* 8: 300–301.
Coupin, H. 1922. *Album général des Cryptogames. Algae. Les algues du globe* 5(1): pl. 285–356. Paris.
Desikachary, T.V. & Sreelatha, P.M. 1989. Oamaru diatoms. *Biblioth. Diatomol.* 19.
De Toni, G.B. 1894. *Sylloge Algarum* 2(3). Patavii.
Doig, A.J. 1967. Further notes on the Oamaru diatomite. *Microscopy* 30: 289–295.
Edwards, A.R. 1991. The Oamaru diatomite. *Paleont. Bull. Wellington* 64: 1–260.
Fenner, J. 1981. *Diatoms in the Eocene and Oligocene sediments off NW-Africa, their stratigraphic and paleographic occurrences.* Dissertation zur Erlangung des Doktorgrades der Mathematisch-Naturwissenschaftlichen Fakultät der Christian-Albrechts-Universität zu Kiel.
—— 1984. Middle Eocene to Oligocene planktonic diatom stratigraphy from deep sea drilling sites in the south Atlantic, equatorial Pacific, and Indian Oceans. *Initial Rep. deep Sea Drilling Proj.* 75: 1245–1271.
—— 1988. Occurrences of pre-Quaternary diatoms in Scandinavia reconsidered. *Meyniana* 40: 133–141.
—— & Mikkelsen, N. 1990. Eocene–Oligocene diatoms in the western Indian Ocean: taxonomy, stratigraphy and paleoecology. *Proc. ocean drilling Progr., Sci. Rep.* 115: 433–463.
Forti, A. 1912. Contribuzioni Diatomologiche. XII.– Metodo di classificazione delle Bacillariee Immobili fondato sull'affinità morfologica dei frustoli ed in relazione con l'evoluzione dell'auxospora. *Atti R. Ist. veneto Sci.* 71: 677–731.
Fryxell, G.A. 1975. Diatom collections. *Beih. nov. Hedwigia* 53: 355–365.
Fuge, D.P. 1937. *Nitzschia firthii* spec. nov., a diatom from Chinese canned fish. *Jl R. microsc. Soc.* ser. 3, 57: 183–185.

Gladenkov, A. Yu. 1991. The Paleogene diatom flora of the Komandorsky Islands (the Bering Sea). *In* H. Simola (Ed.), *Proc. 10th Internat. Diat. Symp.*: 243–247.

Glezer, Z.I. 1969. Pozdneeotsenovye kompleksy diatomovykh, kremnevykh zhgutikovykh vodoroslei i ebriideĭ yugo-zapadnoĭ chasti turgaĭskogo progiba. *Trudy vses. nauchno-issled. geol. Inst.* nov. ser. **130**: 67–85.

—— 1984. Znachenie issledovanii po sistematike diatomovykh vodoroslei dla biostratigrafii i paleografii. *Ezheg. vses. paleont. Obshch.* **27**: 284–298.

—— Jousé, A.P., Makarova, I.V., Proshkina-Lavrenk, A.I. & Sheshukova-Poretskaya, V.S. (Eds). 1974. *Diatomovye Vodorosli SSSR, iskopaemye i sovremennye* **1**. Leningrad.

—— Karayeva, N.I., Makarova, I.V., Moiseeva, A.I. & Nikolaev, V.A. 1988. Klassifikatsiya diatomovykh vodoroslei, prinyataya v nastoyashchem izdanii. *In* Z.I. Glezer, I.V. Makarova, A.I. Moiseeva, & V.A. Nikolaev (Eds), *Diatomovye Vodorosli SSSR, iskopaemye i sovremennye* **2**(1): 31–34. Leningrad.

—— Makarova, I.V., Moiseeva, A.I. & Nikolaev, V.A. (Eds). 1992. *Diatomovye Vodorosli SSSR, iskopaemye i sovremennye* **2**(2). Sankt-Peterburg.

—— & Sheshukova-Poretskaya, V.S. 1968. Pozdneeotsenovye diatomovye, zolotistye i peridinievye vodorosli i ebriidei severo-vostochnoi okrainy ukrainskogo krystallicheskogo massiva. *Paleont. Sb. Lemberg* **5**: 117–124.

—————— 1969. K istorii formirovanya pozdneeotsenovoi morskoi diatomoboi flory Ukrainy. *Vest. Leningr. gos. Univ.* **1969**(9): 60–73.

Gombos, A.M., Jr. 1982. Early and middle Eocene diatom evolutionary events. *Bacillaria* **5**: 225–242.

Greuter, W., Barrie, F.R., Burdet, H.M., Chaloner, W.G., Demoulin, V., Hawksworth, D.L., Jørgensen, P.M., Nicolson, D.H., Silva, P.C., Trehane, P. & McNeill, J. 1994. International code of botanical nomenclature (Tokyo code) adopted by the Fifteenth International Botanical Congress, Yokohama, August–September 1993. *Regnum veg.* **131**.

Greville, R.K. 1863. Descriptions of new and rare diatoms. Series X. *Q. Jl microsc. Sci.* new ser. **3**: 227–237, pl. IX, X.

—— 1866. Descriptions of new and rare diatoms. Series XX. *Trans. microsc. Soc. Lond.*, new ser. **14**: 121–130, pl. XI, XII.

Grove, E. & Sturt, G. 1886. On a fossil marine diatomaceous deposit from Oamaru, Otago, New Zealand, Part I. *J. Quekett microsc. Club* ser. 2, **2**: 321–330, pl. XVIII–XIX.

—— 1887a. On a fossil marine diatomaceous deposit from Oamaru, Otago, New Zealand, Part III. *J. Quekett microsc. Club* ser. 2, **3**: 63–78, pl. V–VI.

—— 1887b. On a fossil marine diatomaceous deposit from Oamaru, Otago, New Zealand, Appendix. *J. Quekett microsc. Club* ser. 2, **3**: 131–148, pl. X–XIV.

Grunow, A. 1887. Referat über Grove, E. and Sturt, G., On a fossil marine diatomaceous deposit from Oamaru, New Zealand. *Bot. Zbl.* **31**: 131–133.

—— 1888. Referat über Grove, E. and Sturt, G., On a fossil marine diatomaceous deposit from Oamaru, New Zealand. ... Part III and appendix. *Bot. Zbl.* **34**: 34–41.

Hajós, M. 1986. A Magyarországi miocén diatomás képzodmények rétegtana. Stratigraphy of Hungary's miocene diatomaceous earth deposits. *Geologica hung., Ser. palaeont.* **49**: 1–339.

Hamilton, C.W. & Reichard, S.H. 1992. Current practice in the use of subspecies, variety, and forma in the classification of wild plants. *Taxon* **41**: 485–498.

Hanna, G.D. 1928a. The Monterey shale of California at its type locality with a summary of its fauna and flora. *Bull. Am. Ass. Petrol. Geol.* **12**: 969–983, pl. 7–10.

—— 1928b. The age of the diatom-bearing shales at Malaga Cove, Los Angeles County, California. *Bull. Am. Ass. Petrol. Geol.* **12**: 1109–1111.

—— 1929. Fossil diatoms dredged from the Bering Sea. *Trans. S. Diego Soc. nat. Hist.* **5**(20): 287–296.

—— 1931. Diatoms and Silicoflagellates of the Kreyenhagen Shale. *Mining in California* **27**: 187–201.

—— 1936. Notes on localities of fossil diatoms in California. *Bull. Soc. fr. Microsc.* **5**: 109–112.

—— & Grant, W.M. 1926. Expedition to the Revillagigedo Islands, Mexico, in 1925, II. Miocene marine diatoms from Maria Madre island, Mexico. *Proc. Calif. Acad. Sci.* ser. 4, **15**: 115–193.

Hasle, G.R., Stosch, H.A. von & Syvertsen, E.E. 1983. Cymatosiraceae, a new diatom family. *Bacillaria* **6**: 9–156.

Holmes, R. W. & Brigger, A. L. 1979. The marine fossil diatom genus *Entogonia* Greville – a review. *Bacillaria* **2**: 155–214.

Holmgren, P.K., Holmgren, N.H. & Barnett, L.C. 1990. Index herbariorum. Part I: The herbaria of the world. 8th ed. *Regnum veg.* **120**.

Homann, M. 1991. Die Diatomeen der Fur-Formation (Altertertiär) aus dem Limfjord-Gebiet, Nordjütland/Dänemark. *Geol. Jb.* A, **123**: 1–285.

Ichikawa, W. 1960. On the fossil marine diatoms in the Wakura Beds, Noto Peninsula, Japan. *Sci. Rep. Kanazawa Univ.* **7**: 175–214, pl. I–IX.

—— Fuji N. & Bachmann, A. 1964. Fossil diatoms, pollen grains and spores, Silicoflagellates and Archaeomonads in the Miocene Hojuji diatomaceous mudstone Noto Peninsula. Central Japan. *Sci. Rep. Kanazawa Univ.* **9**: 25–118, pl. I–III, Taf. I–VII.

Jenkins, O.P. 1931. Stratigraphic significance of the Kreyenhagen shale of California. *Mining in California* **27**: 141–186.

Jousé, A. 1955. Novye vidy diatomovykh paleogenovogo vozrasta. Species novae diatomacearum aetatis paleogenae. *Notul. syst. Inst. cryptog. Horti bot petropol.* **10**: 81–103.

—— 1979. Diatom biostratigraphic zones of the Eocene. *Beih. nov. Hedwigia* **64**: 427–445.

Jurilj, A. 1965. Neobicni i neistrazeni ure-aji za vezanje u kolonije kod nekih alga. *Acta bot. croat.* **24**: 73–78.

Kanaya, T. 1957. Eocene diatom assemblages from Kellogg and 'Sydney' shales, Mt. Diablo area, California. *Sci. Rep. Tôhoku Univ.* 2nd ser. (Geol.) **28**: 27–124, pl. III–VIII.

—— 1959. Miocene diatom assemblages from the Onnagawa formation and their distribution in the correlative formations in northeast Japan. *Sci. Rep. Tôhoku Univ.*, 2nd ser. (Geol.) **30**: 1–130, pl. 1–11.

Karsten, G. 1928. Abteilung Bacillariophyta (Diatomeac). *In* A.Engler, *Nat. Pflanzenfam.*, Zweite Aufl., **2**: 105–303.

Kozyrenko, T.F. & Sheshukova-Poretskaya, V.S. 1967. Materialy k izucheniyu diatomovykh vodoroslei neogena yuzhnykh Kuril'ckikh ostrovov. *Vest. Leningr. gos. Univ.* **1967**(21) (Biol. 4): 88–104.

Krotov, A.I. & Shibkova, K.G. 1959. Novye vidy diatomovykh iz paleogenovykh diatomovykh otlozheniĭ Urala. Species novae diatomacearum e palaeogeno montium Uralensium. *Notul. syst. Inst. cryptog. Horti bot petropol.* **12**: 112–129.

Laporte, L.-J. 1936. Au sujet de la localisation géographique du dépôt diatomifère de *Santa Monica* et de quelques autres dépôts californiens. *Bull. Soc. fr. Microsc.* **5**: 106–109.

—— & Lefébure, P. 1930. *Diatomées rares et curieuses*. **2**. Paris.

Lautour, H.A. de 1889. On the fossil marine diatomaceous deposit near Oamaru. *Trans. Proc. N.Z. Inst.* **21**: 293–311, pl. XVIII–XXIII.

Lefébure, P. 1935. Diatomées contenues dans le dépôt fossile marin de Saint-Laurent-la-Vernède (Gard). *Bull. Soc. fr. Microsc.* **4**: 44–57, pl. III–IV.

—— 1947. *Atlas pour la détermination des Diatomées*. Paris.

—— & Chenevière, E. 1939. Description et iconographie de diatomées rares ou nouvelles. II. *Bull. Soc. fr. Microsc.* **8**: 21–25, pl. 1.

McLean, H. & Barron, J.A. 1988. A late middle Eocene diatomite in northern Baja California Sur, Mexico: implications for tectonic translation. *In* M.V. Filowicz & R.L. Squires (Eds), Paleogene stratigraphy, west coast of North America. *Pacific Section, Society of Economic Paleontologists and Mineralogists, West Coast Paleogene Symposium* **58**: 1–8.

McCloy, C., Ingle, J.C. & Barron, J.A. 1988. Neogene stratigraphy, foraminifera, diatoms and depositional history of Maria Madre Island, Mexico: evidence of early Neogene marine conditions in the southern Gulf of California. *Mar. Micropaleont.* **13**: 193–212.

Mandra, Y.T. 1968. Silicoflagellates from the Cretaceous, Eocene, and Miocene of California, U.S.A. *Proc. Calif. Acad. Sci.* **36**: 231–277.

Mann, A. 1907. Report on the diatoms of the Albatross Voyages in the Pacific Ocean, 1888–1904. *Contr. U.S. natn. Herb.* **10**: 221–419, pl. 44–54.

Mann, D.G. 1984. Observations on copulation in *Navicula pupula* and *Amphora ovalis* in relation to the nature of diatom species. *Ann. Bot.* **54**: 429–438.

Mills, F.W. 1934. *An index to the genera and species of the Diatomaceae and their synonyms 1816–1932.* **19**: 1401–1480. London.

Möller, J.D. 1891. *Lichtdrucktafeln hervorragend schöner und vollständiger Möller'scher Diatomaceen-Präparate.* Wedel-in-Holstein.

—— 1892. *Verzeichniss der in den Lichtdrucktafeln Möllerscher Diatomaceen-Präparate enthaltenen Arten.* Wedel-in-Holstein.

Monjanel, A.-L. 1987. *Les diatomées Oligocènes à Holocènes de l'Atlantique nord et de la Méditerranée occidentale: biostratigraphie et paléocéanographie.* Université de Bretagne Occidentale (Thése), Brest.

Oakley, K.P., Campbell, B.G. & Molleson, T.I. (Eds) 1975. *Catalogue of fossil hominids. Part III: Americas, Asia, Australasia.* London.

Okamura, K. 1911. Some littoral diatoms of Japan. *Rep. imp. Fish. Inst. Tokyo* **7**(4): 1–18, pl. VIII–XIII.

Okuno, H. 1952. *Atlas of fossil diatoms from Japanese diatomite deposits.* Kyoto.

Ol'shtynskaya, A.P. 1978. Novye diatomovye vodorosli (Bacillariophyta) pozdnego eotsena Ukrainy. *Paleont. Sb. Lemberg* **15**: 75–79.

Pantocsek, J. 1886. *Beiträge zur Kenntniss der fossilen Bacillarien Ungarns.* I Theil: Marine Bacillarien. Nagy-Tapolcsány.

—— 1889. *Beiträge zur Kenntniss der fossilen Bacillarien Ungarns.* II Theil: Brackwasser Bacillarien. Anhang Analyse der marinen Depôts von Bory,

Bremia, Nagy-Kürtös in Ungarn; Ananino und Kusnctzk in Russland. Nagy-Tapolcsány.

—— 1892. *Beiträge zur Kenntniss der fossilen Bacillarien Ungarns*. III Theil: Süsswasser Bacillaricn. Anhang: Analysen 15 neuer Depôts von Bulgarien, Japan, Mähren, Russland und Ungarn. Nagy-Tapolcsány.

—— 1905. *Beiträge zur Kenntniss der fossilen Bacillarien Ungarns*. III Theil.: (Beschreibung der auf Tafel 1–42 abgcbildeten Arten). Pozsony.

Peragallo, M. 1903. *Catalogue général des Diatomées*. Livr. 53, pp. 804–818. Clermont-Ferrand.

Pritchard, A. 1861. *A history of the Infusoria including the Desmidiaceae and Diatomaceae, British and foreign*. 4th ed. London.

Proshkina-Lavrenko, A.I., Jousé, A.P., Kisilev, A.I., Poretskii, V.S. & Sheshukova, V.S. 1949. *Diatomovyi Analiz*. 2. Opredelitel' iskopaemykh i sovremennykh diatomovykh vodoroslei. Poryadki Centrales i Mediales. Leningrad.

Reinhold, T. 1937. Fossil diatoms from the Neogene of Java and their zonal distribution. *Verh. geol.-mijnb. Genoot. Ned., Geol. Ser.* 12: 43–133, pl. 1–21.

Robinson, J.H. 1936. The occurrence and distribution of the diatoms in the Oceanic Beds of Barbados. *J. Barbados Mus*. 3: 149–152.

—— 1937. The occurrence and distribution of the diatoms in the Oceanic Beds of Barbados. (III & IV). *J. Barbados Mus*. 4: 180–183.

—— 1938. The occurrence and distribution of the diatoms in the Oceanic Beds of Barbados – V. *J. Barbados Mus*. 5: 144–150.

—— 1941a. The occurrence and distribution of the diatoms in the Oceanic Beds of Barbados. (VI). *J. Barbados Mus*. 8: 84–86.

—— 1941b. The occurrence and distribution of the diatoms in the Oceanic Beds of Barbados. (VII). *J. Barbados Mus*. 8: 181–185.

Ross, R. 1972. On some fossil species of *Hemiaulus*. *Trans. Proc. bot. Soc. Edinb.* 41: 323–342.

—— 1976. Some Eocene diatoms from South Atlantic cores. Part II. *Rutilaria* Greville. *Occ. Pap. Calif. Acad. Sci.* 123: 21–27.

—— 1990. Spinivinculum, a new genus of centric diatoms. *Beih. nov. Hedwigia* 100: 263–275.

—— Cox, E.J., Karayeva, N.I., Mann, D.G., Paddock, T.B.B., Simonsen, R. & Sims, P.A. 1979. An amended terminology for the siliceous components of the diatom cell. *Beih. nov. Hedwigia* 64: 513–533.

—— & Sims, P.A. 1972. The fine structure of the frustule in centric diatoms: a suggested terminology. *Br. phycol. J.* 7: 139–163.

—— —— 1973. Observations on family and generic limits in the Centrales. *Beih. nov. Hedwigia* 45: 97–121, pl. 1–7.

—— —— 1985. Some genera of the Biddulphiaceae (diatoms) with interlocking linking spines. *Bull. Br. Mus. nat. Hist.* (Bot.) 13: 277–381.

Round, F.E., Crawford, R.M. & Mann, D.G. 1990. *The diatoms, biology & morphology of the genera*. Cambridge.

Schmidt, A.F.W. 1889. *Atlas der Diatomaceenkunde*. Heft 35–36. Taf. 137–144. Leipzig.

—— 1892. *Atlas der Diatomaceenkunde*. Heft 43–44. Taf.169–176. Leipzig.

Schrader, H.-J. 1969. Die pennaten Diatomcen aus dcm Obereozän von Oamaru, NeuSeeland. *Beih. nov. Hedwigia* 28: 1–124, Taf. 1–39.

—— 1978. Diatoms in DSDP leg 41 sites. *Initial Rep. deep Sea Drilling Proj.* 41: 791–812.

—— & Fenner, J. 1976. Norwegian Sea Ccnozoic diatom biostratigraphy and taxonomy. Part 1 Norwegian Sea Cenozoic diatom biostratigraphy. *Initial Rep. deep Sea Drilling Proj.* 38: 921–1099.

Schütt, F. 1896. Bacillariales (Diatomeae). *In* A. Engler & K. Prantl, *Nat. Pflanzenfam.* 1(1b): 31–150.

Sheshukova-Poretskaya, V.S. 1967. *Neogenovye morskie diatomovye vodorosli Sakhalina i Kamchatki*. Leningrad.

—— & Glezer, Z.I. 1964. Novye vidy morskikh paleogenovykh diatomovykh vodorosleï USSR. Diatomeae marinae novae e paleogeno Ucrainiae. *Nov. Sist. Nizsh. Rast.* 1964: 78–92.

Shipboard Scientific Party. 1974. Sitc 214. *Initial Rep. deep Sea Drilling Proj.* 22: 119–191.

Simonsen, R. 1972. Ideas for a more natural system of the centric diatoms. *Beih. nov. Hedwigia* 39: 37–54.

—— 1979. The diatom system: ideas on phylogeny. *Bacillaria* 2: 9–71.

Sims, P.A. 1986. *Sphynctolethus* Hanna, *Ailuretta* gen. nov., and evolutionary trends within the Hemiauloideae. *Diatom Res*. 1: 241–269.

—— 1988. The fossil genus *Trochosira*, its morphology, taxonomy and systematics. *Diatom Res.* 3: 245–257.

Smith, H.L. 1872. Conspectus of the families and genera of the Diatomaceae. *Lens* 1: 1–19.

Stosch, H.A. von. 1975. An amended terminology of the diatom girdle. *Beih. nov. Hedwigia* 53: 1–35.

Strel'nikova, N.I. 1974. *Diatomei pozdnego Mela (Zapadnaya Sibir')*. Moskva.

—— 1987. *Paleogenovye diatomovye vodorosli vysokikh shirot severnogo i yuzhnogo polusharii*. Leningrad.

—— 1988. Paleogenovye diatomovye vodorosli priantarktichcskogo raiona atlantichcskogo i tikhogo okcanov. *In* V.A. Krasheninnikov & I.A. Basov (Eds), *Morska stratigrafiya i mikropaleontologiya*: 128–148. Moskva.

Taylor, F.B. 1929. *Notes on Diatoms*. Bournemouth.

Tempère, J. 1893. Remarques sur lcs diatomées de Hongrie du Dr Pantocsck. Avec listes rectificatives par MM. J. Brun et E. Baxter. *Diatomiste* 2: 29–54.

—— & Peragallo, H. 1893. *Diatomées. Collection J. Tempère et H. Peragallo*. Fasc. 17. pp.253–264. Paris. [Whilst the title page, the fascicle covers and the labels of the accompanying slides read 'Diatomées. Collection J. Tempère & H. Peragallo', this set of exsiccata is advertised in *Le Diatomiste*, published by Tempère, as 'Les Diatomées du Monde entier' and this is the title usually used in bibliographies.]

—— —— 1908. *Diatomées du Monde entier. Collection Tempère et Peragallo* (2e edition). Fasc. 4. pp. 49–64. Arcachon. [This edition is entitled 'Diatomécs du Monde enticr' throughout.]

—— —— 1912. *Diatomées du Monde entier. Collection Tempère et Peragallo* (2e cdition). Fasc. 23. pp. 353–368. Arcachon.

Truan y Luard, A. & Witt, O. N. 1888. *Die Diatomaceen der Polycystinenkreide von Jérémie in Hayti, Westindien*. Berlin.

Tsumura, K. 1964. Some kinds of *Rutilaria* and *Pseudorutilaria*. *Bull. Yokohama City Univ. Soc.* 16 (Nat. Sci. 1): 77–99.

Van Heurck, H. 1883. *Synopsis des Diatomées de Belgique*, Atlas, Heft 6. Pl. 104–132, 22 bis, 82 bis, 83 bis, 83 tcr, 95 bis. Anvers.

—— 1896. *A treatise on the Diatomaceae*, translatcd by Wynne E. Baxter. London.

—— 1899. *Traité des Diatomées*. Anvers.

Vanlandingham, S.L. 1978. *Catalogue of the fossil and recent genera and species of diatoms and their synonyms*. 7. Vaduz.

Walker, W.C. & Chase, H.H. 1887. *Some new and rare diatoms*. Series II, III. Flint, Michigan.

Whiting, M.C. & Schrader, H.-J. 1985. Late Miocene to early Pliocene marine diatom and silicoflagellate floras from the Oregon coast and continental shelf. *Micropaleontology* 31: 249–270.

Williams, D.M. 1988. An illustrated catalogue of the type specimens in the Greville diatom herbarium. *Bull. Br. Mus. nat. Hist.* (Bot.) 18: 1–148.

Woodring, W.P. & Bramlette, M.N. 1950. Geology and paleontology of the Santa Maria District California. *Prof. Pap. U.S. geol. Surv.* 222: 1–183.

Wornardt, W.W. 1967. Miocene and Pliocene diatoms from California. *Occ. Pap. Calif. Acad. Sci.* 63: 1–108.

Yanagisawa, Y., Nakamura, K., Suzuki, Y., Samamura, K., Yoshida, F., Tanaka, Y., Honda, Y. & Tanahashi, M. 1989. Tertiary biostratigraphy and subsurface geology of the Futuba district, Joban coalfield, northeast Japan. *Bull. geol. Surv. Japan* 40: 405–467.